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CONTENTS

Sudanian Elements in the Flora of Israel *A. Shmida & J. A. Aronson* 1

Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus *Geoffrey A. Levin* 29

Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic Analysis *Geoffrey A. Levin* 86

Notes on the Floral Biology of *Couroupita guianensis* Aubl. (Lecythidaceae) *Sonia Yarsick, Nerida Xena de Enrech, Nelson Ramirez, & Getulio Agostini* 99

Convergent Evolution of the '*Homeria*' Flower Type in Six New Species of *Moraea* (Iridaceae–Irideae) in Southern Africa *Peter Goldblatt* 102

The Calyx in *Lycianthes* and Some Other Genera *W. G. D'Arcy* 117

Serotaxonomy of *Solanum, Capsicum, Dunalia,* and Other Selected Solanaceae *Richard N. Lester & Philip A. Roberts* 128

Notes on the Systematics of *Hesperantha* (Iridaceae) in Tropical Africa *Peter Goldblatt* 134

Cytology and Systematics of the *Moraea fugax* Complex (Iridaceae) *Peter Goldblatt* 140

Notes on Peruvian Palms *Alwyn H. Gentry* 158

A Guide to Collecting Palms *John Dransfield* 166

MISSOURI BOTANICAL
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VOLUME 73
SPRING 1986
NUMBER 1

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SUDANIAN ELEMENTS IN THE FLORA OF ISRAEL[1]

A. SHMIDA[2] AND J. A. ARONSON[3]

ABSTRACT

In the Dead Sea Rift Valley of Israel, a northern tongue of penetration of Sudanian elements exists that has traditionally been regarded as composed of Miocene relicts. We postulate that most of these elements have penetrated the area since the end of the Pleistocene. The principal habitats harboring Sudanian elements in Israel are described, including the pseudo-savanna in wadi beds, cliffs and rock formation, oases and in the Dead Sea Rift as well as a variety of secondary habitats outside the Rift. In addition, a statistical analysis of the 116 species in the flora of Israel considered to be Sudanian elements is presented, covering growth form, phytogeographic distribution, dispersal mechanisms, and degree of endemism. Special attention is given to the arboreal elements, including 49 species of trees, shrubs, and perennial vines. A comparison is made between the habitats of these species in East Africa and in Israel: significant habitat shifts were found in some cases. Although paleo-macrofossils are almost non-existent in the area, other evidence, such as low degree of endemism, disjunctiveness, and adaptations to aridity and long-distance dispersal indicate that the great majority of the Sudanian elements in the Dead Sea Rift are of recent origin. The relationships between the typical evergreen Mediterranean elements with paleotropical origins and the extant Sudanian elements in Israel are discussed.

Within the portion of the Syrian-African Rift lying between the Red Sea to the south and the watershed of the Jordan River in the Golan Heights, a large number of Sudanian elements, plants as well as animals, are found considerably farther north than anywhere else in their distribution range and in many cases growing under ecological conditions quite different from their norm. In addition, a handful of Sudanian species also occur in the low-lying coastal plain of Israel, almost entirely cut off from the Dead Sea Rift Valley and the bulk of the Sudanian region proper (Fig. 1). Climatic and geological conditions in the Dead Sea Rift Valley explain in part the pres-

[1] A. Shmida wishes to express his considerable debt of gratitude to the late Prof. M. Zohary who introduced him (and dozens of other students) to the intricacies and unique attributes of the Israeli flora. We thank G. E. Wickens who reviewed the manuscript with meticulous care, helped gather information for some of the distribution maps, and made valuable suggestions for improvement of the text. J. B. Gillett and P. Quézel also kindly reviewed the manuscript and provided stimulating comments and suggestions. Our thanks also go to Sandy Greenberg, Seemah Shemesh, and Marion Milner who provided computer and typing assistance, to Nancy R. Morin and Dr. Marjorie Tiefert for patient and professional editorial guidance, and to Miri Shmida who drew the figures. The assistance of J. Dransfield in preparing Figure 5 is gratefully acknowledged. Any errors or inaccuracies therein are entirely the responsibility of the authors. Finally we thank the numerous guides of the Israeli Society for the Protection of Nature who helped us locate some of the rare and little-known populations of Sudanian plants in Israel. We gratefully acknowledge financial assistance received during the course of this research from the Bath-sheva de Rothschild Fund to A. Shmida and the Clifford M. Hardin Fund of the Fund for Higher Education to J. A. Aronson.

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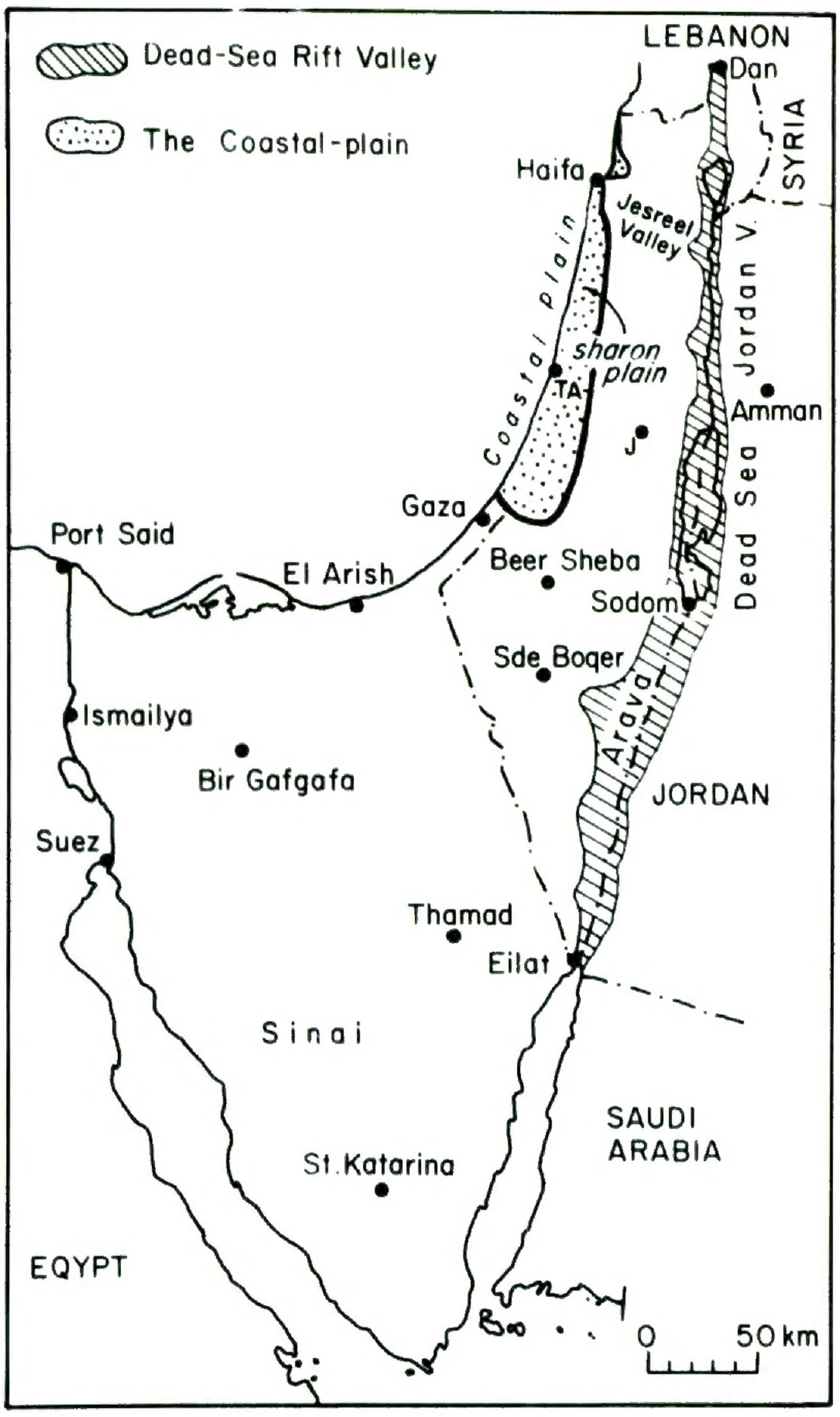

FIGURE 1. General geographical aspect of the study area with the main districts harboring Sudanian elements.

ence of Sudanian species so far north, but several questions remain concerning the present ecological adaptations and distribution patterns of the Sudanian elements in Israel. The most intriguing of these is simply: how and when did these species, whose principal distribution is in subtropical Africa and similar regions in Arabia and the Thar Desert of India and West Pakistan reach Israel particularly in the Dead Sea Rift Valley?

Only two papers relating directly to the Sudanian floristic elements in Israel can be found in the literature. One is Eig's work, in which he cites about 170 species of plants from the Dead Sea Rift Valley, of which more than 30% are Sudanian (Eig, 1931–1932). The second paper (Gruenberg-Fertig, 1954) is a renewed and detailed phytogeographical analysis of the Sudanian species in Palestine with particular emphasis on the affinities of those elements to the Eritreo-Arabian and West-Sudanian subregions of Engler (1879–1882) and others.

Since the publication of Eig's and Gruenberg-Fertig's works, our knowledge of the vegetation of Israel and its neighboring areas has increased greatly. This is due mainly to the publication of new floras of Israel (Zohary & Feinbrun-Dothan 1966–1974; Feinbrun-Dothan, 1978, 1985), Egypt (Täckholm, 1974), the Sahara (Ozenda, 1977), the Thar Desert (Bhandari, 1978), and others (e.g., Wickens, 1977; Lind & Morrison, 1974; Danin, 1983). We have to date recorded more than 800 species of plants growing in the Dead Sea Rift Valley, of which 14.5% can be considered Sudanian elements. More ecological information concerning the Sudanian elements in Israel outside the Dead Sea Rift Valley has also been collected, and additional information on the details of the ranges of many Sudanian species has been amassed. Consequently, the conclusions of Eig, Zohary, Gruenberg-Fertig, and others on the age and origin of the Sudanian elements in Israel should be reconsidered.

The dominant view of this question, as presented by Zohary (1973), Tchernov (1968), and others has held that the Sudanian elements in Israel, both within the Dead Sea Rift Valley and along the coastal plain, are Miocene relicts surviving in specialized habitats from an earlier, warmer, and wetter period when tropical vegetation occurred as far north as central Europe.

The opposing view, held by Tristram (1884), Hart (1891), and Bodenheimer (1935), argues that the Sudanian elements in Israel are recent and arrived in Israel in waves during the warm intervals that occurred during the Pleistocene, i.e., during the last million years. Galil (1972) revived this theory and even went so far as to suggest that most of the Sudanian plants occurring in Israel today are the result of the most recent penetration that took place in the hyperthermic period about 4,000 to 8,000 years ago.

The purpose of this paper is to enlarge on and analyze the findings related to the Sudanian elements in Israel and to attempt to resolve the issue of the relative age of the extant Sudanian vegetation in Israel. Since fossil records relevant to this discussion are essentially non-existent, we will attempt to apply ecological theory and phytogeographical analysis to elucidate the issue. Furthermore, we can compare the local situation with that of nearby regions that have already been analyzed, e.g., the Saharo-North African Region studied by Monod (1957), Ozenda (1977),

Quézel (1958, 1965, 1978), and others as well as recent general studies of the vegetation of Africa, such as those by Knapp (1973) and White (1976, 1983), and of nearby regions including Iran (Hedge & Wendlebro, 1978) and Arabia (Mandaville, 1984).

The Environment—Geomorphology and Climate

The Dead Sea Rift Valley (Fig. 1), which is subdivided into the Jordan Valley and the Arava Valley, is part of the northern section of the Syrian-African Rift that extends from northern Syria southwards through the Red Sea, terminating in East Africa (Garfunkel, 1970, Freund & Garfunkel, 1978). This rift is a relatively new feature that has been slowly widening since Oligocene-Miocene times (Freund 1965, Freund et al., 1970). During this period, the Arabian Peninsula and Jordan have moved at least 40 km northwards with respect to Egypt, the Sinai, and Israel (Freund et al., 1968). Since the Pliocene, this movement has led to the concomitant formation of a deep rift so that the rivers that once drained from Transjordan into the Mediterranean Sea now drain into the Dead Sea Rift from Dan in the north to the central Arava in the south.

The Dead Sea Rift is defined by two large fault systems running in a north–south direction that border it on the west and east. These systems have caused the formation of large cliffs and steep inclines on either side of a deep depression (Garfunkel & Horowitz, 1966; Neev & Emory, 1967). Climatically, this depression constitutes a rain-shadow desert, the intensity of which is determined by the abrupt difference in altitude (ca. 100 m) between the valley floor and the mountains to the west, beyond which most of the rain fronts originate.

Rainfall throughout the Middle East decreases from north to south, and the precipitation gradient in the area under discussion decreases from 600 mm annually in the Dan area in the north of Israel to 27 mm in the Eilat area in the south (Anonymous, 1970). In keeping with this, distinct changes in vegetation zones are observed, from the extreme xeric vegetation in the Arava (south) through the steppe vegetation in the Jericho-Beit Shean area (central) to the Mediterranean vegetation in the Hula Valley area (north) (Fig. 2). The more intense the rain-shadow formed in the Dead Sea Rift Valley the further north the xeric vegetation zones penetrate. Accordingly, xerophytic desert vegetation in the rain-shadow area of the Judean Desert penetrates as far north as Wadi Auja, and Irano-Turanian steppe vegetation penetrates up to the Mt. Gilboa area.

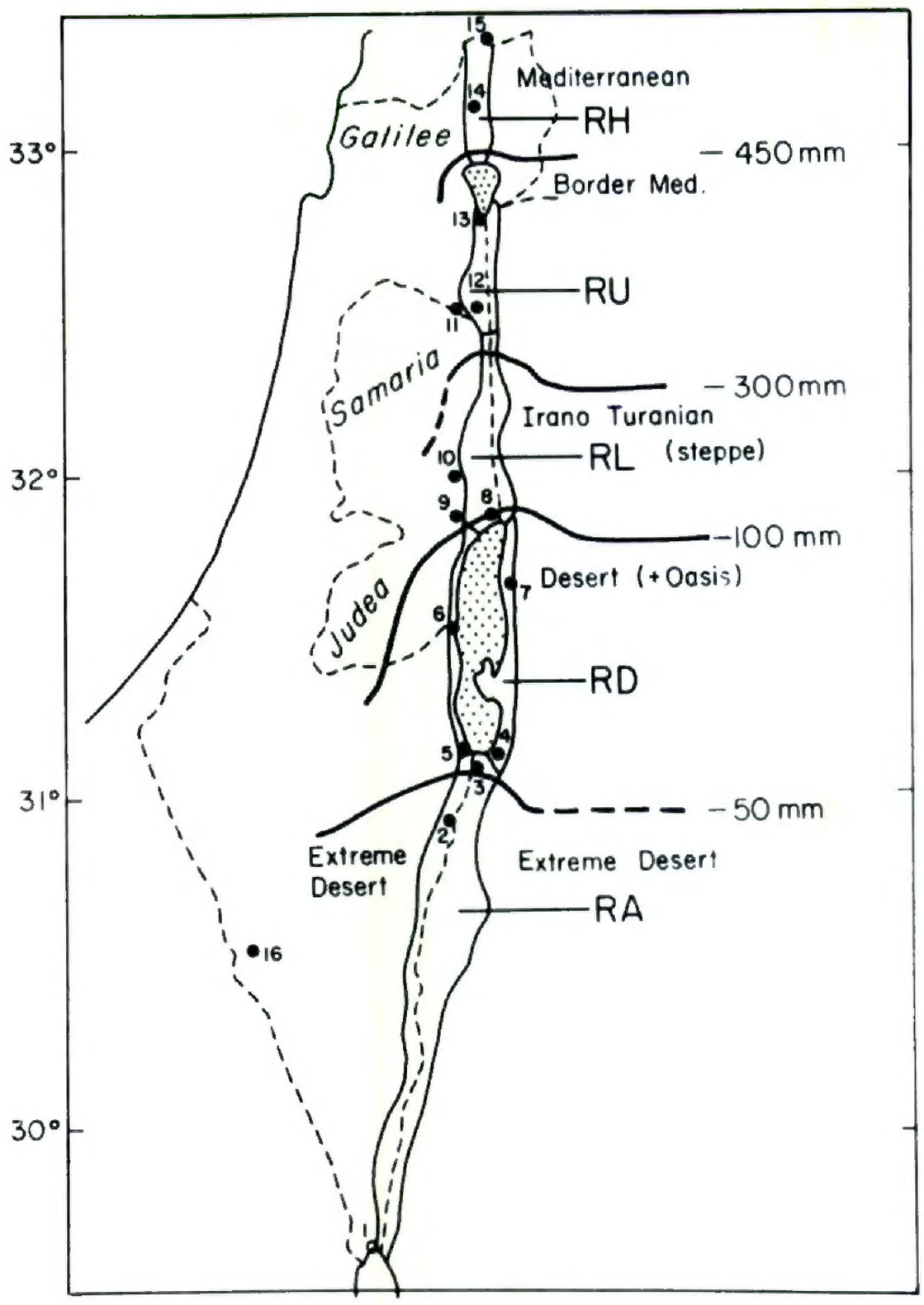

FIGURE 2. Dominant phytogeographical regions within the Dead Sea Rift Valley (modified after Zohary, 1973) and mean annual rainfall isohytes.

Because the flora and fauna inhabiting the slopes descending to the Dead Sea Rift Valley have also been influenced by the sharp depression of the Syrian-African Rift, these slopes are considered part of the Dead Sea Rift Valley for this paper. Like other typical geomorphological depressions, the Dead Sea Rift includes wide alluvial valleys, some draining to the Red Sea and some with underground drainage systems in which salt marshes and saline springs have formed. Large fault and contact springs have led to the formation of extensive oases that are characteristic of the fault escarpment area. Thus, four habitat types exist in the Dead Sea Rift that can support Sudanian floristic (and faunal) elements, as will be discussed in detail below. The great majority of Sudanian species occurring in Israel are found in one or more of these habitats.

Outside the Dead Sea Rift, a smaller number of Sudanian elements are found in a variety of

habitats throughout the low-lying plains and valleys of the coastal and inland regions. The two important outlying districts that support Sudanian elements, i.e., the Dead Sea Rift and the coastal plain, are separated by the mountainous regions of Judea, Samaria, and the Galilee (Fig. 2). However, a sparse transitional zone does exist between the two in southern Israel from the Arava Valley through the northern Negev to the coastal plain. Moving north and west along this transitional zone, the Sudanian elements are increasingly restricted to distinctly thermic habitats such as southern exposures. The abundance of these elements decreases along the zone with the exception of the hydrophilic species, which are most abundant in the coastal plain.

THE PALEOGEOGRAPHY AND PALEOECOLOGY OF THE DEAD SEA RIFT VALLEY

During the Eocene a tropical climate prevailed in the latitudinal subtropical belt of the world (Zohary, 1973; Axelrod & Raven, 1978). As a result, tropical vegetation dominated in the Mediterranean basin and as far north as central Europe and England as indicated by fossilized leaves and fruits of tropical trees found in those areas. These fossils belong to the paleophytogeographical Laurosilvia geoflora (Takhtajan, 1969; Zohary, 1973). The tropical forests of southeast Asia are the largest and most representative areas in which elements of this vegetation have survived today (Zohary, pers. comm.; Thorne, pers. comm.).

Great changes took place during the Miocene (Axelrod, 1975). Along with the Alpine orogenesis, desertification and disintegration occurred in the subtropical belt, and the tropical vegetation retreated towards the equator. At this time, the Tethys Sea, which had covered large areas of the Middle East and central Asia, shrank and was replaced by large steppe areas (Tchernov, 1975). The process of desertification continued throughout the Pliocene, which was, however, a much colder period than the Miocene. The principal development of the steppe flora of central Asia (including many Chenopodiaceae, Artemisia, and other typical Irano-Turanian representatives) is believed to have occurred then. This flora penetrated to north Africa through the Middle East and reached the coast of the Spanish Sahara. During the Pliocene a branch of the Mediterranean Sea penetrated through the Jezreel Valley of Israel and formed a saline lake in the central and upper Jordan Valley (Horowitz, 1979).

During the Pleistocene, extreme fluctuations between rainy and dry periods occurred in the subtropical belt. During the last cycle it was colder and rainier in Israel than at present by some 3–4°C in temperature and an undetermined amount of less average annual precipitation (Horowitz, 1979).

Following the end of the Wuram period in the Middle East about 17,000 years ago (Bar Yosef, 1975), a trend towards warmer, drier conditions began, reaching present levels by about 8000 B.C. Since then, during the Holocene, very few major climatic changes are believed to have taken place (Horowitz, 1979). Around 6000 B.C., a brief hyperthermic period occurred and approximately 4000 B.C., a colder one (the Atlantic period) (Nir & Bar Yosef, 1976).

Until the Pliocene, the Dead Sea Rift Valley was a shallow depression that did not interfere with the flow of rivers from Transjordan to the Mediterranean Sea (Garfunkel & Horowitz, 1966). Since then, the drastic deepening of the Dead Sea Rift by faults on both sides resulted in the formation of the Judean Desert area, a rain-shadow desert, and the thermophilic, arid-tropical conditions of the Dead Sea Rift Valley, particularly around the Dead Sea (Neev & Emory, 1967).

This historical geographical description has been derived from geological and geomorphological evidence and not from direct botanical evidence. Israel is extremely poor in plant fossils: the only two finds in this field after the Mesozoic era are leaves of tropical species found in Miocene formation in the Yemin Plain and Hatzeva (Lorch, 1966). This suggests that the climate in that period in the Negev and Dead Sea Rift was more tropical. Zoological evidence from the Miocene-Pliocene period is also rather poor but increases from the end of the Pliocene to the present (Tchernov, pers. comm.).

DEFINITION AND DELINEATION OF THE SUDANIAN PHYTOGEOGRAPHICAL REGION

The Sudanian phytogeographical region constitutes one of the most problematic in the Old World in terms of classification and delineation. Grisebach (1884) classified all of tropical Africa as a "Sudanian" zone. Subsequently, throughout the last century, there have been several attempts to further delineate the arid and semi-arid re-

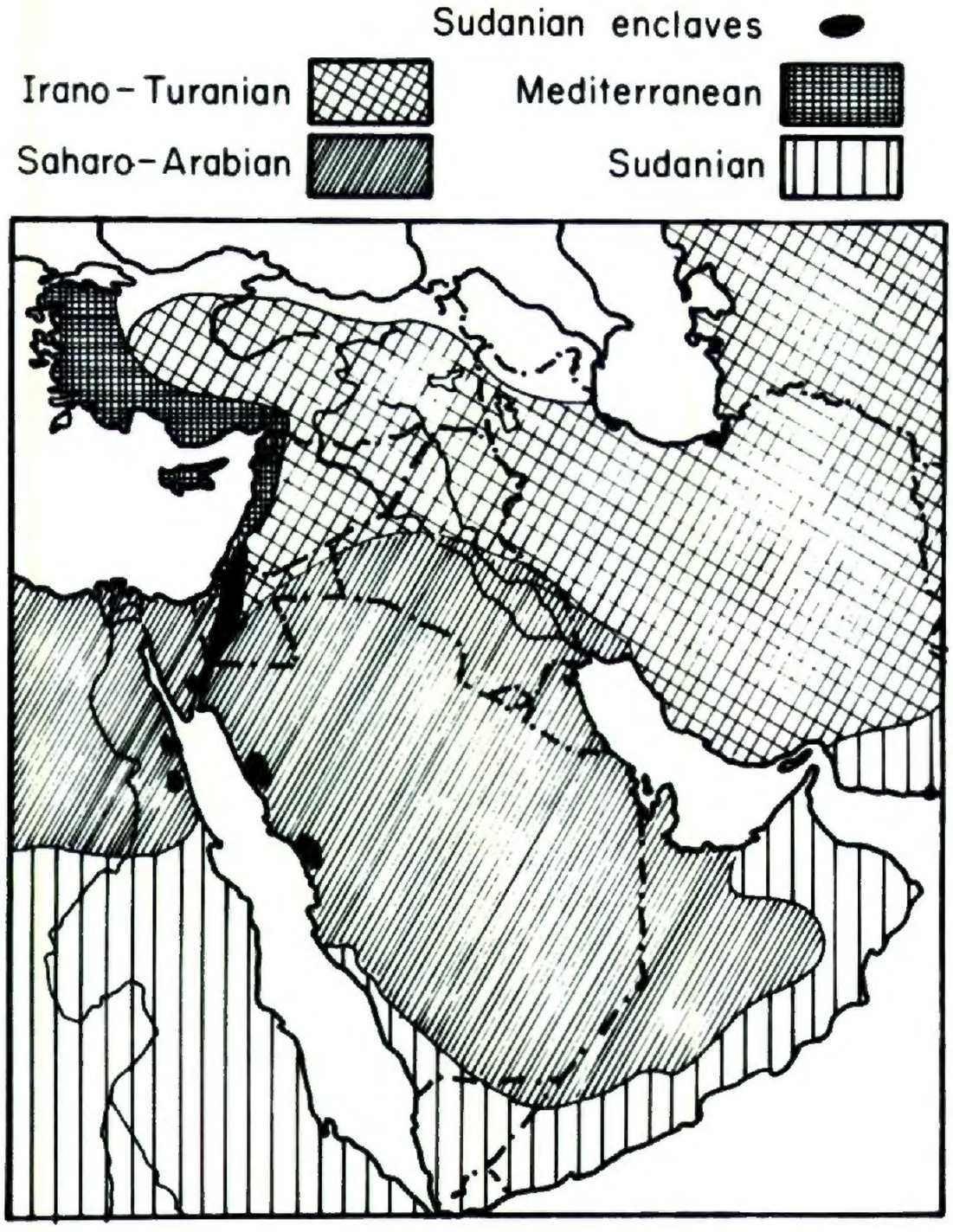

FIGURE 3. Phytogeographical regions relevant to the study area (modified after Zohary, 1973). Note the striking penetration of the Sudanian elements northward along the Dead Sea Rift Valley.

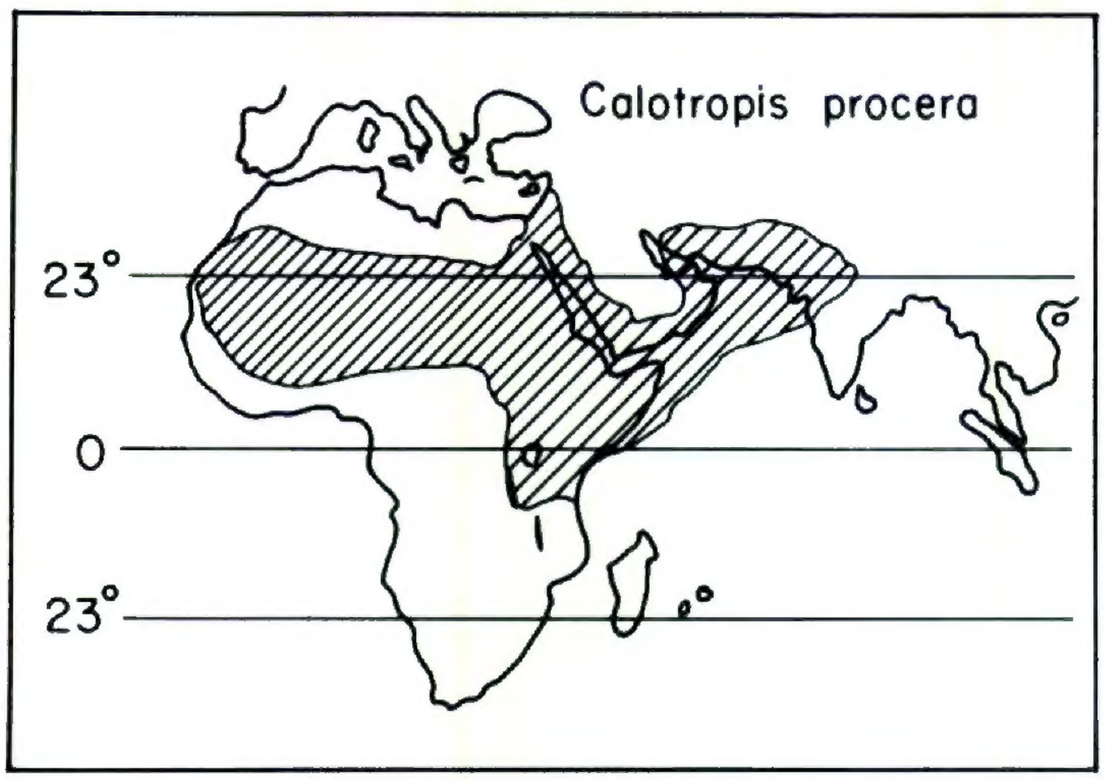

FIGURE 4. Distribution map of *Calotropis procera* that represents a typical Sudanian distribution (sensu Zohary, 1973).

gions in Africa and relevant regions of the Middle East and the Indian subcontinent (Engler & Drude, 1896; Chevalier, 1938; Eig, 1938; Good, 1964; Meyer-Homji, 1965; Burtt, 1971; Zohary, 1973; Werger, 1973; Wickens, 1977; Werger & Coetzee, 1978; Hedge & Wendlebro, 1978; Walter, 1979; White, 1967, 1983; Mandaville, 1984).

Eig (1938), who was the first to study in detail the phytogeographical regions of and relevant to the Middle East, defined a "Sudano-Deccanian region" that included a relatively narrow belt in west Africa and a much broader portion of east and northeast Africa, thence across the Red Sea, around coastal Arabia, and eastward to the Deccan Plateau in central India. Concomitantly, he combined the region of Sind (western Pakistan), northwest India (principally Rajasthan), and parts of Baluchisthan and southern Iran with the hyper-arid Sahara Desert that lies roughly in the same latitudes. This broad region he called "Saharo-Sindian."

Zohary (1945, 1963, 1973) revised Eig's scheme by combining the "Sindian" region with the African and Arabian parts of Eig's "Sudano-Deccanian region," while including the Deccan Peninsula in the Saharo-Arabian portion of Eig's "Saharo-Sindian region." For simplicity, Zohary called the results of this switch the "Sudanian" and "Saharo-Arabian" phytogeographical regions, respectively (Figs. 3, 4).

Gruenberg-Fertig (1954) and Monod (1957) also questioned the affinity between the Deccan flora and that of the Saharan and Arabian regions. Both of these authors commented on Eig's own recognition of the relative individuality of the flora of the semi-arid Deccan Peninsula as compared with the rest of his "Sudano-Deccanian region." In 1965, Meyer-Homji categorically rejected the validity of a "Sudano-Deccanian region" and proposed instead a "Sudano-Rajasthanian region," because "it is the semi-arid Rajasthan which offers closer analogies with the Sudan region, by consideration of the bio-climatic conditions and the ombrothermic diagrams." More significantly from our point of view, Meyer-Homji (1965) showed that "the strength of the so-called Sudano-Deccanian element in the entire southern semi-arid zone [of India], including the Deccan, is only 2.6%," while in the northern semi-arid zone (i.e., Rajasthan and adjacent parts of Gujerat and Punjab), "it is two times higher (5.6%)."

Unfortunately, in the same paper Meyer-Homji (1965) supported the use of Eig's term "Saharo-Sindian" to combine the Saharo-Arabia region with Sind sensu stricto, that is, the Indus River Valley to the west of Rajasthan. Thus, additional confusion was created concerning the division of the macro-regions in question.

Eig's term "Saharo-Sindian" was again revived in a recent paper by Hedge and Wendlebro (1978) dealing with southern Iran. These authors argued moreover, that this term should also be

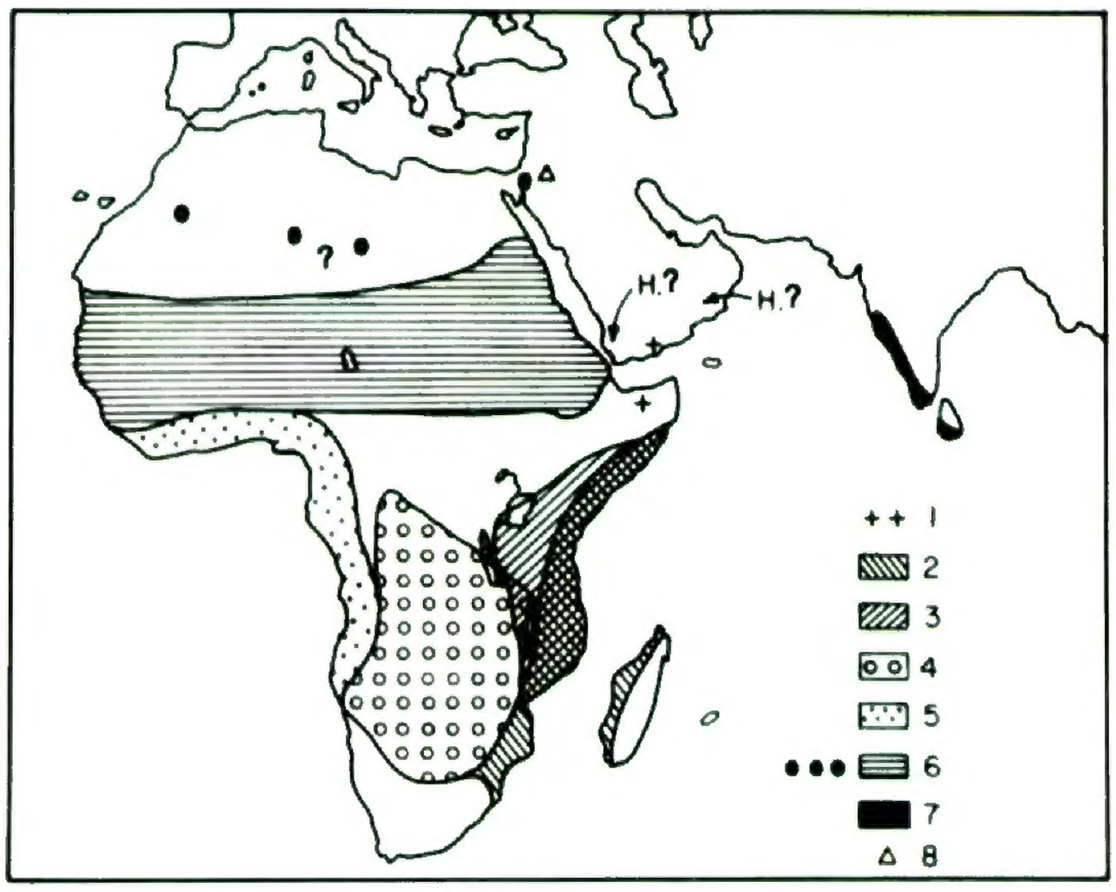

FIGURE 5. The genus *Hyphaene*, which represents a Sudanian-Zambesian distribution (sensu Werger, 1978). Key: 1 = *H. reptans*, 2 = *H. coriacea*, 3 = *H. compressa*, 4 = *H. petersiana*, 5 = *H. guineensis*, 6 = *H. thebaica*, 7 = *H. dichotoma*, 8 = *H. sinaitica* (the only record; the distinction of this taxon from *H. thebaica* is not recognized by Feinbrun-Dothan, 1985).

used to describe the portion of southern Iran described by Zohary (1973) as "Sudanian." Based on their observations in southern Iran, Hedge and Wendlebro cast doubt on the validity of describing any of the species in southern Iran as "Sudanian elements." Instead, they maintained that most of the prominent species grouped by Zohary, Eig, and others under the rubric of "Sudanian elements" could be better classified as "east-west tropical African/Arabian" elements (Hedge & Wendlebro, 1978: 456). "The species of this element," they wrote, "are very widely dispersed with no clear pattern other than being widely dispersed in subtropical and tropical parts of the Old World. In Iran, they grow quite intermixed with the species of the north African/Arabian element," which is the name they proposed in place of Zohary's "Saharo-Arabian" elements.

In striking contrast, Mandaville (1984) recently offered strong support for Zohary's phytogeographic terminology, including the concept of a "Sudanian" group of elements. He even went so far as to propose an extensive enlargement of the territory delineated by Zohary as "Sudanian" in Arabia. According to Mandaville (1984), not just the coastal regions, but nearly two-thirds of the Arabian Peninsula should be classified as "Sudanian," at the expense of the "Saharo-Arabian" territory as defined by Zohary (1973).

We believe that outside of Africa, and most certainly on the temperate fringes of the distribution of the basically tropical elements under discussion, it is not at all surprising to find "Sudanian" elements intermingling with the numerically more significant eremaic Saharo-Arabian and/or other local elements. In Israel the same situation is found, as will be described in detail below.

Within Africa itself, White (1983) has confirmed the existence of a "Sudanian regional center of endemism," one of only seven such centers that he recognizes for the entire continent (he points out that it is the "least unambiguously defined" of the centers of endemism by his criteria). By contrast, the Sahelian region is treated by White as one of a number of regional transitional zones, "showing gradual replacement of one flora with another that is little complicated by endemism" (White, 1983: 43). We will follow White in this matter, rather than Chevalier (1938) and Greenway (1970) who recognized a "Sahelien zone" per se, or Le Houerou and Popov (1981) among others who speak of a "Sudano-Sahelien zone."

Burtt (1971) has emphasized the strong floristic similarity between the semidesert floras of the Sudanian region (sensu Zohary, 1973) and those of the southern half of Africa. Accordingly, Burtt recognized an amalgamated "Sudano-Zambesian phytogeographical region," which was supported and discussed in more detail by Werger (1973) and Werger and Coetzee (1978) (see Fig. 5). It is worth noting that this concept corresponds with Engler's original scheme of 1879–1882. We realize that strong affinities exist between the semidesert and savanna floras of the southern and northern halves of Africa and therefore acknowledge the validity of Burtt's terminology. We argue, however, that given the current sketchy state of knowledge, phytogeographic delineation in Africa is still largely a matter of perspective and individual opinion. Until a careful computerized analysis can be undertaken of the floristic and genetic components of the various regional floras under discussion, no hard and fast nomenclature can be agreed upon. In the meantime, we choose to follow Zohary's and White's general concept (if not all specific details) of the Sudanian phytogeographical region. We choose this course not only for practical reasons but also to provide historical continuity.

In contrast to the lack of agreement on the delineation of the phytogeographical regions under discussion, there is overall agreement concerning the zoogeographic regions (Bodenhei-

mer, 1935; Udvardy, 1969). Two separate zoogeographical regions are consistently distinguished in the Old World: the Ethiopian region in Africa and the Oriental region in Asia.

It is important to emphasize here the striking difference between the phyto- and the zoogeographic regions as defined by biogeographers concerned with the Old World, for it reflects a major distinction between the macro-distribution of animals and plants in the area. Whereas a relatively strong line of demarcation apparently exists between the respective faunas of the African and Asian continents, no such division exists between the two floras.

Above all, we wish to emphasize that our objective here is not to delineate a Sudanian phytogeographic region in Israel, in our view, such an effort is unjustified. Instead we are concerned with the occurrence, distribution, and ecological behavior of the relatively limited number of Sudanian elements that reach our study area. By the same token, we have no desire to enter into taxonomic disputes. With very few exceptions, we follow the taxonomy given in the "Flora Palestina" and other published floras (Zohary & Feinbrun-Dothan, 1966–1974; Feinbrun-Dothan, 1978, 1985) even where it is clear that further taxonomic revision is required.

Typical and Key Determinants of the Sudanian Elements

The Sudanian zone as a whole is typified by plants of tropical origin that have acquired one or more adaptations to relatively hot and arid conditions, yet retain higher demands for moisture than true desert species. The characteristic vegetation type is the savanna—low, open forests of small trees and large shrubs with perennial grasses dominating the open spaces between them (Shmida, 1982). The trees are typically multi-stemmed with sparse, open canopies. Many of them are spiny, with small compound, xeromorphic leaves. Some are evergreen (*Balanites, Maerua, Boscia, Salvadora,* and some *Ziziphus* species) and some are drought-deciduous (e.g., *Acacia, Albizia,* and *Commiphora* (species). Many are characterized by a reduced leaf area, with green stems assuming some of the photosynthetic function. In retamoid (broom-like) shrubs this adaptation is most prominent—the plants being leafless throughout most of the year while the stems become the primary photosynthetic organs. Some examples of this group are *Moringa peregrina, Capparis decidua, Leptadenia pyrotechnica, Ochradenus baccatus,* and *Periploca aphylla.*

Many of the trees have an umbrella shape, which is most striking in *Acacia*—the dominant genus of the Sudanian savannas. Xerophytic vines are occasionally found climbing on the savanna trees (e.g., *Cocculus pendulus, Commicarpus* and *Boerhavia* spp., asclepiad vines such as *Oxystelma esculenta* as well as various perennial cucurbits).

The Sudanian flora in the Dead Sea Rift is typical in its arboreal elements but unusual in lacking a continuous grass cover between the trees. Some Sudanian grasses do occur there—species of *Pennisetum, Cenchrus, Cymbopogon, Enneapogon,* and others. But the overall aspect of the vegetation type in the Dead Sea Rift is best described as a pseudo-savanna, owing to the scarcity of perennial grasses. Moreover, a wide range of non-Sudanian, desert chamaephytes belonging to the Saharo-Arabian phytogeographical region intermingle with the Sudanian elements, creating a kind of bi-regional patchwork or mosaic. In the hammadas or regs and other portions of the Dead Sea Rift where no suitable habitats occur for Sudanian elements, the Saharo-Arabian elements dominate (Zohary, 1962). The same pattern is apparently also found in west and north Africa (Quézel, 1965, 1978).

Statistical Analysis of the Sudanian Flora in Israel in Relation to Growth-forms, Taxonomy, and Global Distribution

A statistical analysis of the flora of Israel (according to Zohary & Feinbrun-Dothan 1966–1974; Feinbrun-Dothan, 1978, 1985, pers. comm.) shows that 157 plant species, out of a total of 2,173 (i.e., 7.2%), belong at least partially to the Sudanian phytogeographic region. Of these, 116 species, or 68.8% of the subtotal, are considered to be predominantly Sudanian in distribution, sensu Zohary (1973) (Table 1). This represents about 5.3% of the total Israeli flora; it is on this group of 116 species that all further statistical analysis will be based.

Most of the species accepted here as Sudanian show either a straightforward Sudanian distribution or chorotype (55.1%) or a bi-regional Sudanian-Saharo-Arabian chorotype [10.3% (SU-SA) + 18.1% (SA-SU) = 28.4%]. In both of these

TABLE 1. Phytogeographical analysis of the Sudanian elements in the flora of Israel and their growth forms [data from the "Flora Palestina" (Zohary & Feinbrun-Dothan, 1966–1974; Feinbrun-Dothan, 1978, 1985) with corrections].

Chorotype[a]	Number	Percent	Trees	Shrubs	Chamaephytes	Hemicryptophyte	Annual	Annual/Facultative Perennial	Vine	Parasite
Sudanian	64	55.1	17.2[b]	18.7	31.3	6.2	14.1	3.1	7.8	1.6
Sudanian-Saharo-Arabian	12	10.3	11.1	11.1	33.3	22.2	11.1	—	11.1	—
Sudanian-Tropical	9	7.7	—	25.0	4.0	4.0	16.0	25.0	—	—
Sudanian-Mediterranean	3	2.6	33.3	—	—	—	33.3	33.3	—	—
Sudanian-Irano-Turanian	3	2.6	33.3	66.6	—	—	—	—	—	—
Pluriregional	4	3.5	—	—	—	25.0	25.0	25.0	—	25.0
Saharo-Arabian-Sudanian	21	18.1	19.1	4.8	33.3	19.1	9.5	14.3	—	—
Total	116	100.0	15.5	16.4	26.7	11.2	15.5	7.7	5.2	1.7

[a] Chorotype = distribution, sensu Zohary (1973).

[b] 17.2 here refers to the percent of species of a particular growth form within the total number of species within the chorotype group, e.g., 11 trees/64 Sudanian = 17.2%.

groups, the high percentage of trees, shrubs, and chamaephytes is especially notable.

Of the eight families most abundant in Sudanian elements in the flora of Israel, five families show significantly higher importance than the reference (meaning a greater percentage contributed by the family in the total number of species in the Israeli flora; see Table 2). These are Chenopodiaceae (5.2% versus 3.2%), Euphorbiaceae (5.2% versus 1.6%), Zygophyllaceae (4.3% versus 0.9%), Asclepiadaceae (6.9% versus 0.7%), and Capparaceae (6% versus 0.4%). The last four of these families have tropical diversity centers (Ozenda, 1977). The higher representation of the Chenopodiaceae in the Sudanian flora than in the reference is perhaps related to the large number of pluriregional chorotypes in this family.

The lower portion of Table 2 reveals the negligible representation of a few typically temperate families in the Sudanian flora of Israel. While the Rosaceae, Ranunculaceae, and Apiaceae have no Sudanian representatives in Israel whatsoever, the Brassicaceae contribute three Sudanian species, which account for 2.6% of the total Sudanian flora in Israel.

Although a total of 92 genera in 40 families are represented, very few genera show large numbers of species with predominantly Sudanian distribution. Only *Acacia* has four species in the group. Five genera have three species each: *Commicarpus, Capparis, Cleome, Moretia,* and *Tamarix.* Ten genera are bitypic and 76 are monotypic. Overall, the mean number of Sudanian species per genus among Sudanian elements in Israel is 1.30, which is quite low relative to the mean number (3.05) of species per genus within the entire flora of Israel.

DISTRIBUTION AND ECOLOGY OF SUDANIAN ELEMENTS IN THE DEAD SEA RIFT VALLEY

The environmental conditions that support Sudanian vegetation in the heart of the Sudanian region in east Africa and the Thar Desert are high ambient temperatures during the growing season, a relatively warm, frost-free winter, and two rainy seasons. The rains come in spring and autumn, with total annual rainfall averaging between 250 and 500 mm (Walter, 1979; Zohary, 1973). In the west African region alternately called Sudanian or Sahelian, a single rainy season occurs in summer, with precipitation averaging 75 to 400 (to 500) mm per year (Wickens, pers. comm.).

The first mentioned determinant of the distribution of Sudanian elements—high year-round temperatures—is found in Israel primarily in the Dead Sea Rift Valley. Accordingly, assuming successful dispersal of diaspores from the Sudanian region to the Dead Sea Rift, or their preexistence there in the past, Sudanian elements should be found in those habitats in the Dead Sea area with moisture regimes similar to those of the main Sudanian region. However, such habitats are relatively very small and scattered.

Moreover, they are specialized habitats that differ ecologically from the true savanna environments of the Sudanian region in Africa.

PRINCIPAL HABITATS OF SUDANIAN ELEMENTS IN THE DEAD SEA RIFT

(1) *Pseudo-savanna in wadi beds and flood plains.* In the large wadi beds of the Arava Valley, *Acacia* species (*A. tortilis* and *A. raddiana*—sometimes described as *A. tortilis* subsp. *raddiana*) dominate the landscape, and a variety of xeric desert species are interspersed among them. We define pseudo-savanna as an association dominated by large savanna trees that can tap the deep year-round ground water available in the wadi beds, but which is virtually lacking the understory of drought-resistant perennial grasses typical of a true savanna. Instead most of the associated species are xeric desert shrubs and annuals such as *Zilla spinosa, Moricandia nitens, Anabasis articulata,* and *Achillea fragrantissima,* all of which belong to the Saharo-Arabian phytogeographic group. The non-arboreal Sudanian elements, as well as most of the shrubs and vines, have migrated up to the cliffs and rocky sites on either side of the Rift Valley. It is important to emphasize that these pseudo-savannas do not cover large areas as they do in Africa but are confined to relatively narrow water courses in flood plains. Zohary (1945) suggested the term "gallery forest" to describe this association; since this term has been extensively used to describe riparian vegetation on the border of the humid tropics (see Wickens, 1977: 30–31), we propose a new term—"Arterial Desert Savanna" for the pseudo-savanna described here. In essence, this term corresponds to the "savane désertique" of Quézel (1965).

(2) *Cliff and rock formations.* Small rock crevices, outcrops, and rocky slopes facing south and east, characterized by warm conditions and a relatively stable water regime, support numerous Sudanian elements, including small shrubs (e.g., *Ephedra foliata*), dwarf shrubs (*Abutilon frutescens*), and perennial grasses (e.g., *Tetrapogon villosus*). In addition, large cliff faces in the fault escarpment along either side of the Dead Sea Rift and scattered throughout the Negev and Sinai provide moist, thermic conditions that support many of the Sudanian species occurring in the area. Important examples are *Capparis cartilaginea, Periploca aphylla,* and *Cocculus pendulus.*

TABLE 2. Relative importance of species numbers within the important families of the Israeli flora and the Sudanian elements within them.[a]

Family	Species in Israel with Predominantly Sudanian Distribution[b]		Total Species in Israel[c]	
	Number	Percent	Number	Percent
Papilionaceae	9	7.7	264	12.1
Compositae	4	3.4	246	11.3
Gramineae	9	7.7	208	9.6
Chenopodiaceae	6	5.2	70	3.2
Euphorbiaceae	6	5.2	34	1.6
Zygophyllaceae	5	4.3	20	0.9
Asclepiadaceae	8	6.9	15	0.7
Capparidaceae	7	6.0	8	0.4
Brassicaceae (Temperate)	3	2.6	115	5.3
Apiaceae (Temperate)	0	0	93	4.3
Rununculaceae (Temperate)	0	0	45	2.1
Rosaceae (Temperate)	0	0	21	1.0

[a] The two columns of the table do not total 100%, because not all the families are included.

[b] The total number of species in Israel with a predominantly Sudanian distribution is 116.

[c] The total number of species in the entire flora of Israel is 2,173.

Some of these species are obligate chasmophytes and they (or vicarious species) grow only on cliffs even in the Sudanian region proper. Examples of these are *Sonchus suberosus* and *Caralluma* spp. Some species that occur only on rocky cliffs in the Dead Sea Rift, however, grow as scrambling climbers supported by *Acacia* and other trees on non-rocky ground in the east African savannas. The outstanding example is *Cocculus pendulus*; other examples are found in *Ephedra* and the *Commicarpus/Boerhavia* complex. In these cases, the habitat of the Sudanian plants has shifted in the more arid environment of the Dead Sea Rift so that their growth conditions, in terms of temperature and water, remain relatively unchanged.

However, for at least a few of the scandent species (e.g., *Oxystelma alpini*), the shift to rocky habitats also represents a shift in growth conditions. In such circumstances, we can say that a niche shift has taken place—a well-known zoological phenomenon (MacArthur, 1972) but one

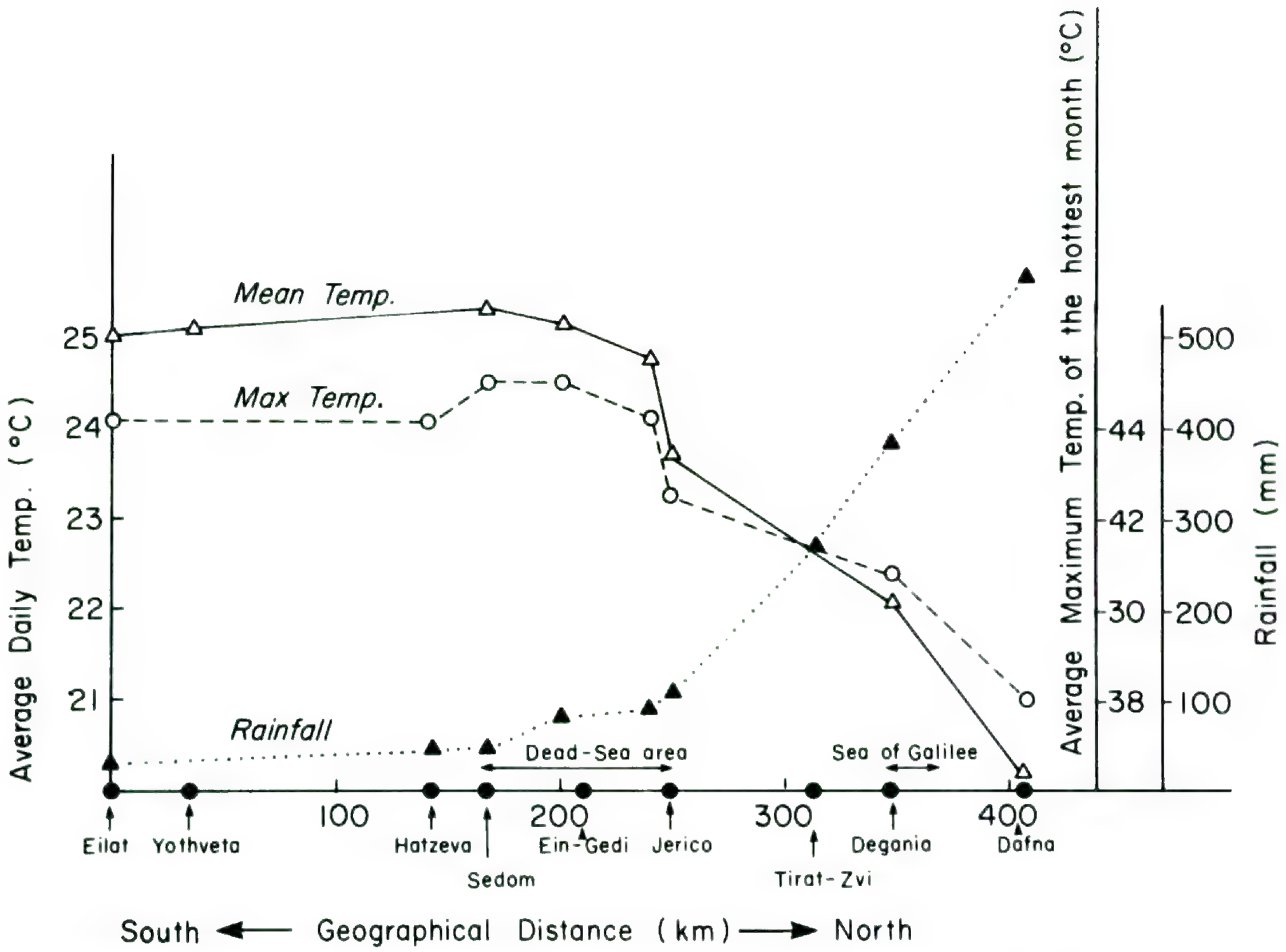

FIGURE 6. Mean annual rainfall and average daily temperature and average maximum temperature along the Dead Sea Rift axis.

so far almost unnoticed in botany (Cody & Mooney, 1978).

(3) *Oases.* The largest concentration of Sudanian species is found in the moist habitats of oases. Species existing in these conditions enjoy both high temperatures and a relative abundance of water. Here can be found arboreal Sudanian species generally uncommon in the Dead Sea Rift due to the rarity of oases. Around the Dead Sea, the major large oases are Ein Gedi, Safi, and Kallirhoi. Sudanian species non-existent in other parts of the Levant (Israel, Lebanon, Syria, and Jordan) grow in these oases. Worthy of mention are *Maerua crassifolia, Capparis decidua, Acacia laeta,* and *Cordia sinensis.*

(4) *Warm salines.* The geomorphological structure of the Dead Sea Rift gives rise to undrained depressions ("Ka"—Evenari et al., 1982) with permanently high ground water where saline conditions occur. In addition, saline habitats occur around the Dead Sea near springs and alluvial fans of large wadis (Zohary, 1945; Zohary & Orshan, 1956).

The majority of the species occurring in these saline depressions are Saharo-Arabian elements; only a few Sudanian taxa are present, yet they are prominent. The species worth noting are *Suaeda monoica, S. fruticosa,* and *Tamarix* spp. These species belong to a peculiar phyto-geographical group (Zohary, pers. comm.) distributed from central Asia all the way to South Africa. They occur throughout the Sudanian (or Sudano-Zambesian) region but are not restricted to it. It is unclear whether their center of origin is Irano-Turanian, Sudanian, or South African. They might even represent part of the "paleo-Welwitchia flora" that connected the ancient deserts of Asia and Africa (Zohary, 1973).

Two additional ancient elements of tropical origin that are concentrated primarily in these saline habitats are the sole two palm species that occur in Israel. The first is the doum palm *Hyphaene thebaica* that, in Israel, grows exclusively in the high-groundwater salt marshes of the southern Arava and along the Gulf of Eilat. The second palm species of Sudanian origin is the date palm *Phoenix dactylifera,* whose center of origin has been a subject of controversy for cen-

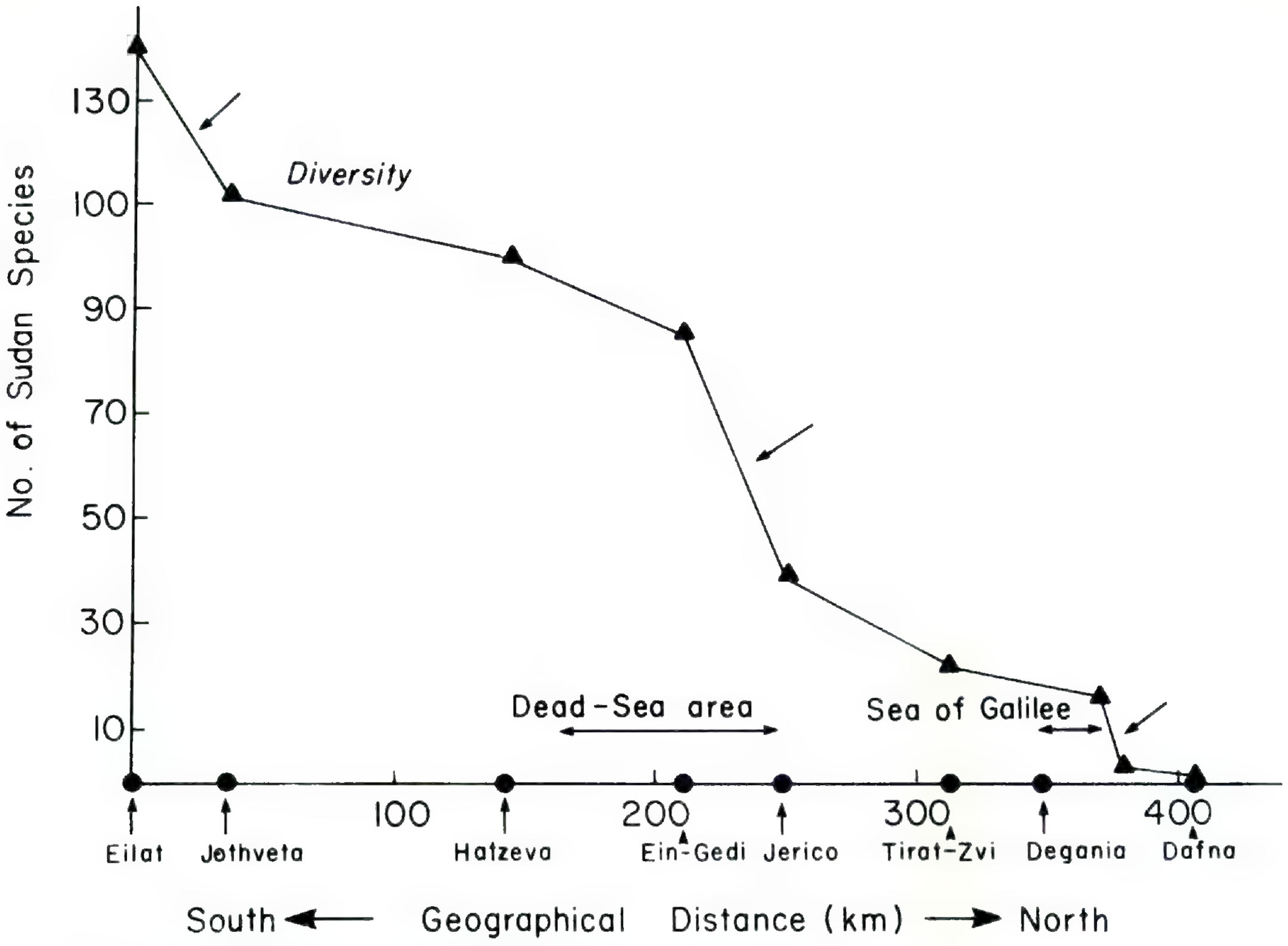

FIGURE 7. Sudanian species diversity along the Dead Sea Rift axis.

turies. As a result of human introduction, cultivated or feral *P. dactylifera* is now found in virtually every desert oasis in Africa, the Middle East, and adjacent regions (Chevalier, 1938; Zohary & Spiegel-Roy, 1975). However, throughout the Saharo-Arabian and Sudanian regions of its present range, it is almost impossible to differentiate between natural and introduced populations. In some of the salines where the species occurs in the Dead Sea Rift Valley, the populations may well be subspontaneous, i.e., escapes from cultivation, but we assume it is indigenous to the area and not an introduction from far away (Zohary, 1982). The salt marshes at Neot HaKikkar and in the Beit Shean Valley might be typical of the kind of natural habitat from which the date palm was originally dispersed to other saline and freshwater springs in nearby desert areas.

DISTRIBUTION PATTERNS AS FUNCTIONS OF ENVIRONMENTAL CONDITIONS ALONG THE DEAD SEA RIFT

Figure 6 illustrates the opposing gradients of mean annual temperatures and precipitation along the length of the Dead Sea Rift. Progressing south from the Dan Valley, the mean annual precipitation decreases from 600 to 27 mm at Eilat (Anonymous, 1970). In contrast, the mean temperatures of the warmest and coldest months increase from 36.4 to 40.2°C in the north and from 7.8 to 10.1°C in the south (Anonymous, 1970).

As described in the preceding section, in areas with insufficient rainfall, the existence of specialized micro-habitats with improved water regimes, combined with the ability of the Sudanian elements to undergo habitat shifts can in part compensate for the overall paucity of precipitation (Boyko, 1947). However, the thermophilic Sudanian elements can only partially contend with low temperatures such as are found north of the Jerusalem-Jericho line, by contracting to southern exposures with increased insolation. Thus, from the standpoint of temperature adaptation, the number of Sudanian species should increase to the south; however, the opposite is true in terms of rainfall requirements. The finding that the overall number of Sudanian species along the Dead Sea Rift decreases from south to north, both absolutely and in relation to the total

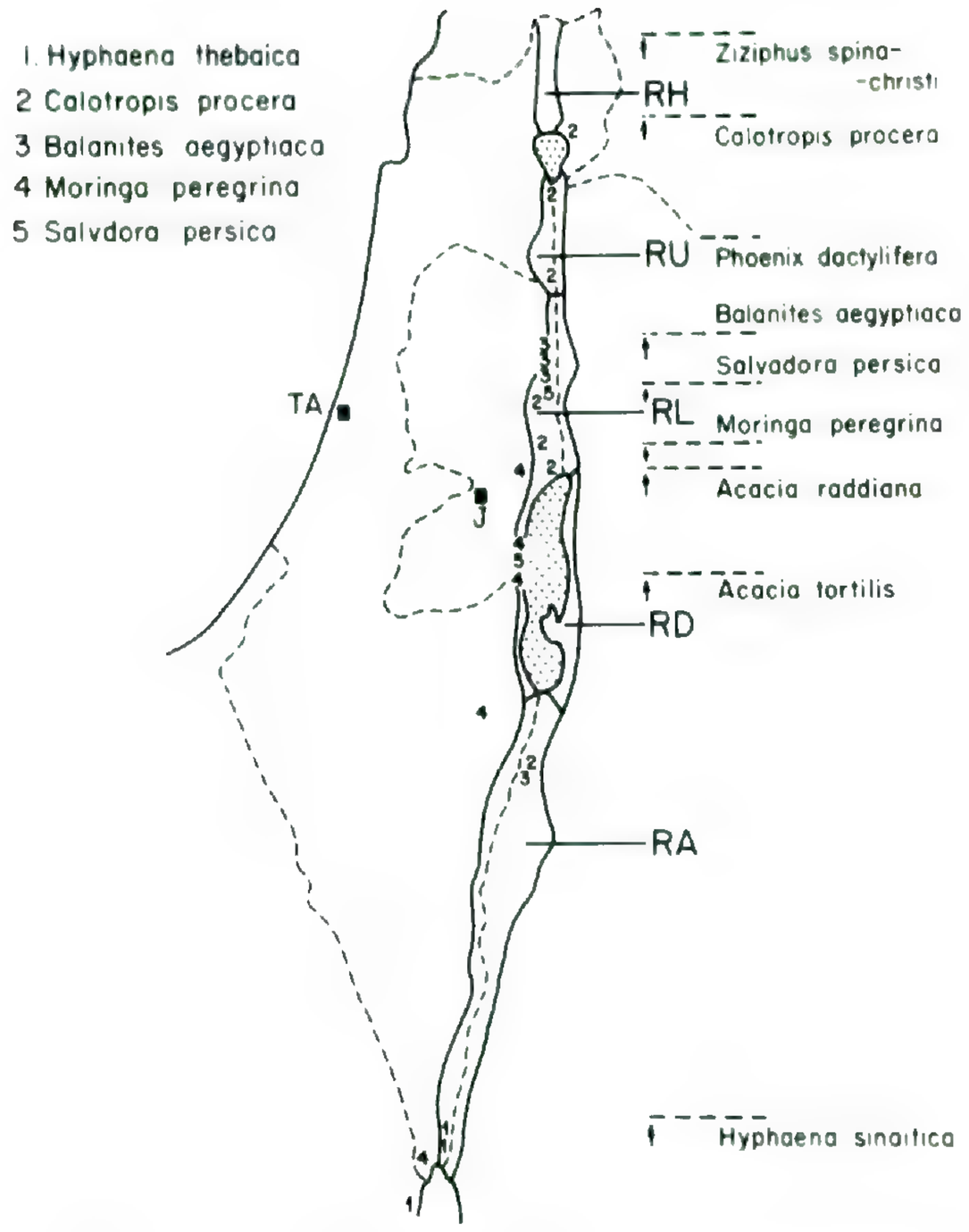

FIGURE 8. Northern distribution borders of typical arboreal Sudanian elements in the Dead Sea Rift. RA—Arava region, RD—Dead Sea region, RL—Lower Jordan Valley, RU—Upper Jordan Valley, RH—Huleh Valley. Numbers indicate solitary distribution points of rare Sudanian trees.

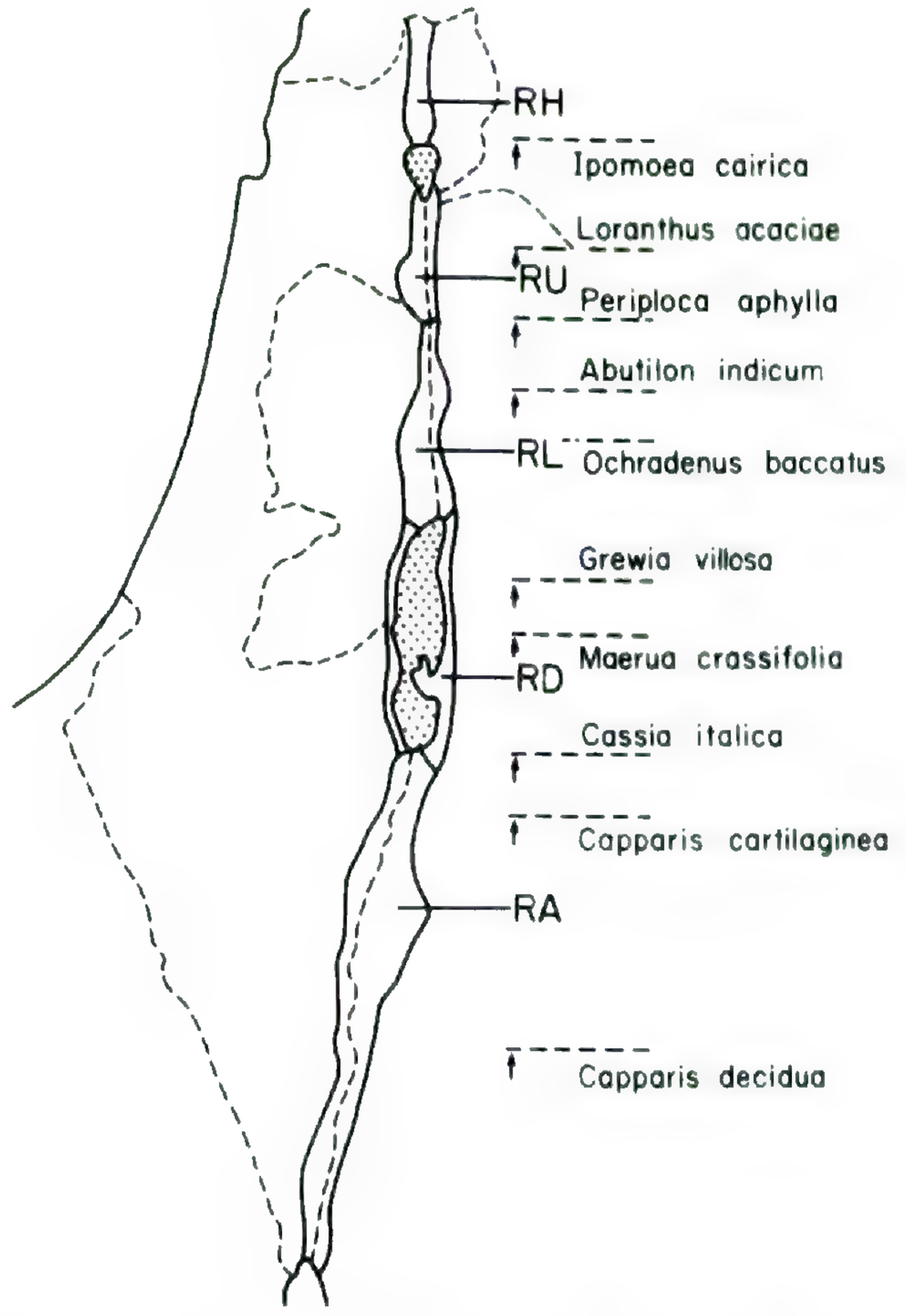

FIGURE 9. Northern distribution borders of small shrubs and woody vines in the Dead Sea Rift Valley.

vegetation cover of the area (Fig. 7), is parallel to the decreasing temperature gradient from south to north.

Figures 8 and 9 show several typical Sudanian species according to their northernmost distribution limit in the Dead Sea Rift. For the purpose of presentation and due to the existence of relatively sharp geomorphological climatic borders along the Rift, we have grouped the plants according to distribution (Table 3). Most of the "Eilat group" are associated with the igneous-metamorphic rock matrix as well as with high temperatures. The distribution of the largest group of Sudanian species ends in the Ein Gedi-Wadi Kelt area (about 20% of the Sudanian species). This may be related to the especially high temperature in this area due to the deep topographical "hole" of the Dead Sea (399 m below sea level) and also to the existence of appropriate habitats such as rocky cliffs and oases. Additional Sudanian species end gradually between the Dead Sea and the Sea of Galilee. The last topographical barrier, the Corrasim Saddle, which rises from the Sea of Galilee (−212 m) to the Hula Valley (30–180 m above sea level), probably presents a drastic climatic change through which none of the Sudanian species have yet broken. North of the Sea of Galilee there are almost no true Sudanian elements. Accordingly, the Rift is the world's northern limit (locus terminus) for most Sudanian species.

There is, however, one phenomenon that seems to contradict the decreasing gradient of Sudanian species from south to north: the population densities of certain Sudanian species increase to the north from the Dead Sea to Mt. Gilboa, where the annual precipitation reached 150–300 mm (Fig. 2). These species, while rare or completely absent from the extremely dry Arava Valley south of the Dead Sea, are common north of it and even form their own communities and dominate the landscape. Three distribution groups are found among these species: (1) plants growing near springs, mainly around the Dead Sea, e.g., *Salvadora persica, Balanites aegyptiaca,* (2) cliff vegetation such as *Periploca aphylla, Sonchus tuberosus,* and *Iphiona maris-mortui,* and (3) plants growing in rock crevices that absorb large amounts of runoff water, such as *Moringa peregrina, Grewia villosa,* and *Abutilon indicum.*

These three habitats are more common around the northern end of the Dead Sea (due to its

special geomorphology) than in other regions of the Rift. Thus, the frequency of the habitats here can explain the "abnormal" abundance of the Sudanian species around the Dead Sea itself.

TAXA ENDEMIC TO THE DEAD SEA RIFT VALLEY

Species in small enclaves outside their main area of distribution have a higher probability of speciation (Stebbins, 1952, 1971) so that an ancient population cut off from its principal area of distribution for thousands or even millions of years may differentiate to the species or even genus level. By contrast, a population isolated for only some hundreds or thousands of years can be expected to differentiate only to the level of forms or varieties, if at all.

Thus one method for determining whether the Sudanian vegetation in the Dead Sea Rift is a Miocene relict or the result of recent invasion is to compare the degree of speciation of Sudanian species in the Dead Sea Rift Valley with that of (1) related taxa in the Sudanian region of east Africa and (2) species from other phytogeographical regions growing in the Dead Sea Rift Valley, such as true desert elements.

Another rule of thumb used by many biogeographers is that the more ancient and isolated the vegetation in an enclave, the greater the chances of finding systematic relicts in it (Shmida, 1985). Thus, if Sudanian vegetation has been present in the Dead Sea Rift since the Miocene, at least some relict taxa with no close systematic relatives and whose distribution areas do not extend outside the Dead Sea Rift, should be found. This is a phenomenon known from other similarly isolated regions, such as the Inyo region in southern California, where many relicts have been recorded (Reveal, 1976; Raven, 1977). For a detailed probability analysis of these two biogeographic rules see Shmida (1985).

We find systematic relicts almost totally absent from the area. This fact is striking in view of the seemingly ideal conditions for speciation in which the various Sudanian species occur in the Rift Valley (small, remote, and disjunct populations subject to extreme desert stress, see Stebbins, 1952). A possible exception is *Trichodesma boissieri,* a chasmophyte endemic to the region between Ein Gedi and Mt. Gilboa. This species is unrelated to others in the genus found in the Dead Sea Rift and Sinai (*T. africana* and *T. ehrenbergii*) and is probably both a systematic and geographic relict. *Trichodesma boissieri* may continue southwards to Yemen through the Arabian Peninsula, but this area is one of the least investigated in the Old World, and no data are available.

Table 4 presents the list of species endemic to the Dead Sea Rift. Only four of them are of certain Sudanian origin and they are limited to the Sdom-Wadi Kelt area. Thirteen species are endemic to the Dead Sea Rift and the Judean Desert and are not of Sudanian origin but derived from other, nearby phytogeographic regions. Most of the endemic species (except for *Trichodesma boissieri*) have allopatric sibling relatives with continuous morphological changes in intermediate populations nearby. *Sonchus suberosus* (Feinbrun-Dothan, 1978) may be another paleoendemic but, owing to its uncertain pre-taxonomic position (compare Boulos, 1962), its taxonomic-evolutionary position is unclear. This pattern hints at the relative youth of the speciation process in the Dead Sea Rift area. If the populations in this area had been isolated from each other for many thousands of years, clear morphological disjunctions would be expected within pairs of main species. If that were the case, the gradual geographical-morphological transition between them would not be discernible at present. We might also expect to see, in at least some of the species, the additional evolutionary step of sympatric expansion and differentiation to different niches. (There are many such examples recorded for other regions, see Mayr, 1970; MacArthur, 1972). Yet none of the species endemic to the Dead Sea Rift or Sudanian species in Israel follows this pattern.

Among Sudanian trees and shrubs, no varieties and certainly no species endemic to the Dead Sea Rift have been found, with the sole exception of *Maerua crassifolia* var. *maris-mortui* (Zohary, 1955). However, it is worth remembering that the speciation process of arboreal species is slower than that of herbaceous and annual ones (Stebbins, 1971; Davis & Heywood, 1963). Most of the arboreal Sudanian species in Israel have very large geographic ranges, from the southern Sahara through southern Arabia to southern Iran and India (Fig. 2). Examples are *Calotropis procera, Capparis decidua, Cassia italica, Grewia villosa, Maerua crassifolia,* and *Ochradenus baccatus.* Some of these taxa spread even further south along the east African savannas to South Africa (Werger, 1978). The distribution of the genus *Moringa* (Fig. 10) exemplifies this distribution pattern. The distribution maps of the ge-

TABLE 3. Geographical distribution of some Sudanian elements in Israel.[a]

Northern Limit of Distribution in the Dead Sea Rift			
Eilat District	Hatzeva District	Dead Sea (Ein Gedi) District	Jericho—Wadi Kelt District
Anticharis glandulosa	*Bothriochloa ischaemum*	*Abutilon hirtum*	*Abutilon fruticosum*
Astragalus sparsus	*Crotalaria aegyptiaca*	*Acacia tortilis*	*A. hirtum*
Cassia senna	*Laisiurus scindicus*	*Capparis decidua*	*Acacia raddiana*
Cleome chrysantha	*Leptadenia pyrotechnica*	*Cleome droserifolia*	*Aerva persica*
Cometes abyssinica	*Leysera leyseroides*	*Convolvulus glomeratus*	*Aizoon canariense*
Eremopogon foveolatus	*Pentatropis spiralis*	*Cordia sinensis*	*Chrozophora oblongifolia*
Glossonema boveana	*Oxystelma alpini*	*Grewia villosa*	*Cleome amblyocarpa*
Hyphaena thebaica	*Tephrosia apollina*	*Hibiscus micranthus*	*Forsskaolea tenacissima*
Lindenbergia sinaica		*Maerua crassifolia*	*Iphonia mucronata* subsp. *maris-mortui*
Monsonia heliotropioides		*Pergularia tomentosa*	*Lavendula pubescens*
Moretia canescens		*Pulicaria inuloides*	*Moringa peregrina*
Otostegia schimperi		*Stipagrostis hirtigluma*	*Ochradenus baccatus*
Pterogaillonia calycoptera		*Zygophyllum simplex*	
Pycnocycia tomentosa			
Seetzenia orientalis			
Tephrosia nubica			

nus *Balanites* (Fig. 11) and *Salvadora* (Fig. 12) illustrate different kinds of distribution patterns within the Sudanian group.

In conclusion, the extant environmental and genecological conditions in the Dead Sea Rift Valley are potentially ideal for speciation (Stebbins, 1952; 1972). The Sudanian species there are represented by small isolated populations, separated by thousands of kilometers from their center of distribution in east Africa. In comparison to prevailing conditions in the east African savannas, many of the habitats of these species have changed drastically, and the species survive under extremely arid climatic conditions. All these factors are indicative of exceptionally strong selective pressures that should have led to rapid speciation within the isolated populations (Stebbins, 1972). However, just the opposite has occurred in the Dead Sea Rift Valley. Very few species have undergone speciation, and when they have, it is only to the variety or subspecies level. In contrast, a relatively high rate of endemism occurs in the Judean Desert, which borders the Dead Sea Rift Valley, consisting mainly of Saharo-Arabian and Irano-Turanian species. These distribution and speciation patterns seem to support the argument that the Sudanian elements in Dead Sea Rift Valley are of recent origin.

DISTRIBUTION AND ECOLOGY OF THE SUDANIAN ELEMENTS IN ISRAEL OUTSIDE THE DEAD SEA RIFT

The distribution of a few Sudanian species in Israel is not limited to the Dead Sea Rift and the thermic wadis of the Negev but also extends into the Mediterranean region (see Fig. 2). These more widespread species represent only about 10% of the Sudanian elements in Israel, but their ecological "behavior" and distribution patterns shed additional light on the question of the relative antiquity of all the Sudanian elements in Israel.

The majority of the Sudanian elements occurring outside the Dead Sea Rift are found primarily in disturbed secondary habitats created, or at least heavily influenced, by human activity. This fact has led to the formulation of the widely accepted theory, expressed by Zohary (1973), that these species, once limited to the Arava Valley in the southern portion of the Dead Sea Rift and to the few scattered oases and saline marshes in the Rift, gradually spread north and west over large areas of the country; this expansion was made possible by the greatly intensified agricultural and settlement activities of the last century. However, some clear and some apparent exceptions to this rule are recognizable, namely in the group of Sudanian aquatic elements and the few

TABLE 3. Continued.

Northern Limit of Distribution in the Dead Sea Rift		Species Penetrating into the Mediterranean Region		
Beit Shean District	Sea of Galilee District	Fully Integrated Elements	Ruderals	Aquatics and Hygrophiles
Balanites aegyptiaca *Cucumis prophetarum* *Loranthus acaciae* *Periploca aphylla* *Salvadora persica* *Trichodesma boissieri*	*Bocopa monnieri* *Calotropis procera* *Commicarpus verticillatus* *Ipomoea cairica* *Tricholaena teneriffae*	*Aristida sieberiana* *Commicarpus africanus* *Desmostachya bipinnata* *Epipactis consimilis* *Hyparrhenia hirta* *Ipomoea cairica* *Pennisetum setaceum* *Ziziphus spina-christi*	*Chrozophora tinctoria*[b] *Withania somnifera*[b]	*Bacopa monnieri* *Cyperus jeminicus* *Nymphaea cerula* *Vigna lutea*

[a] Only well-documented unambiguous cases are included.

[b] These species are included here despite the fact that Zohary (1973) did not record its chorotype as Sudanian, since its Sudanian vicariads are very close—both geographically and systematically. Therefore we assume that it is an instance of a recently derived species of Sudanian origin.

species that appear to be fully integrated today with the predominant Mediterranean vegetation in the coastal plain. The three groups of the Sudanian elements—Ruderals, Aquatics and Hydrophiles, and Fully Integrated—will be discussed in turn, along with an Anomalous group.

RUDERALS

The most prominent of the Sudanian elements that has rapidly expanded and continues to expand into disturbed sites outside the Dead Sea Rift is the so-called Syrian Christ-Thorn, *Ziziphus spina-christi.* The present distribution of this tree, whose edible fruits are dispersed by birds and mammals, includes the valleys of the central plain and Galilee and even some low-lying regions of the central Negev. Within the Rift, it extends all the way to the Dan Valley, i.e., farther north than any other Sudanian arboreal element in Israel. However, a striking dichotomy occurs within the different portions of this extended distribution area. In the Rift Valley up to the Sea of Galilee and in the southern part of the coastal plain, *Z. spina-christi* is evergreen. By contrast, in areas north of the Sea of Galilee and in the northern portion of the coastal plain, it is winter deciduous (Danin, pers. comm.). We hesitate to call the corresponding areas primary and secondary habitats for *Z. spina-christi,* but there can be little doubt that the colder areas to the north represent areas into which *Ziziphus* has recently spread, and is continuing to spread, particularly along roadsides and in abandoned fields. By contrast, the part of the coastal plain where the tree is evergreen may be—together with the southern part of the Rift Valley—part of the species "primary" or natural distribution area in Israel. (For this reason, *Ziziphus* is discussed again below in the section on fully integrated elements.)

Several additional ruderal species among the Sudanian elements are found in the Gramineae. The Sudanian grasses *Hyperrhenia hirta* and *Pennisetum setaceum,* to take two major examples, were formerly limited to southern exposures in the Rift Valley. As a result of intensified human activity, they have recently spread over large areas of the Mediterranean region (Litav, 1967). They are especially dominant along roadsides in low-lying areas along the coastal plain. The northerly penetrations of these grasses

TABLE 4. List of the endemic plant species restricted to the Dead Sea Rift Valley.

Endemic Species	Vicarious Species from Which it Probably Originated	Chorotype of the Parent Taxa	Habitat	Type of Distribution and Speciation
1. *Anthemis maris-mortui*	*A. hebronica*	Irano-Turanian	Thermic slopes	Allopatric distribution with gradual transition
2. *Blepharis attenuata*	*B. ciliaris*	Sudanian	Thermic slopes	Parapatetic distribution with transitions
3. *Centaurea lanata*	*C. aegyptiaca*	Saharo-Arabian	Rocks & wadis of Judean Desert	Allopatric distribution, no transition observed
4. *Fagonia grandifolia*[a]	*F. mollis*	Saharo-Arabian	Slopes of Judean Desert	Allopatric distribution with gradual transition
5. *Galium hierochuntinum*	*G. judaicum*	Mediterranean	Rocks & wadi beds in canyons	Allopatric distribution with gradual transition
6. *Hammada eigii*	*H. scoparia*	Irano-Turanian	Slopes & colluvium	Allopatric distribution with disjunction
7. *Heliotropium maris-mortui*	*H. rotundifolium*	Irano-Turanian	Slope of Judean Desert	Allopatric distribution with gradual transition
8. *Iphiona maris-mortui*[b]	*I. mucronata*	Sudanian	Cliffs & rocks	Allopatric distribution with disjunction of tens of km
9. *Kickxia judaica*	*K. acerbiana*	E. Saharo-Arabian	Cliffs & rocks	Allopatric distribution with gradual transition
10. *Matthiola aspera*	*M. livida*	Saharo-Arabian	Slopes of Judean & Jericho Desert valley	Allopatric distribution with gradual transition
11. *Podonosma syriaca*	*P. syriaca* var. *typica*	Mediterranean	Rocks	Allopatric distribution with gradual transition
12. *Sonchus suberosus*[b]	*S. suberosus* ssp. *suberosus*	Sudanian	Cliffs & canyons	Allopatric distribution with disjunction of hundreds of km
13. *Reseda maris-mortui*[a]	*R. boissieri*	Saharo-Arabian	Thermic slopes	Allopatric distribution with gradual transition
14. *Silene oxydonta*[b]	?	Irano-Turanian	In wadi beds	?
15. *Suaeda asphaltica*	?	Saharo-Arabian-Irano-Turanian	Chalky slopes	No transition
16. *Tamarix palaestina*	*T. jordanis*	Irano-Turanian	Wet habitat	Allopatric distribution
17. *Trichodesma boissieri*	?	Sudanian	Rock outcropping	No transition or allied

[a] The taxonomical rank of these taxa has recently been lowered to varieties.
[b] Very rare.

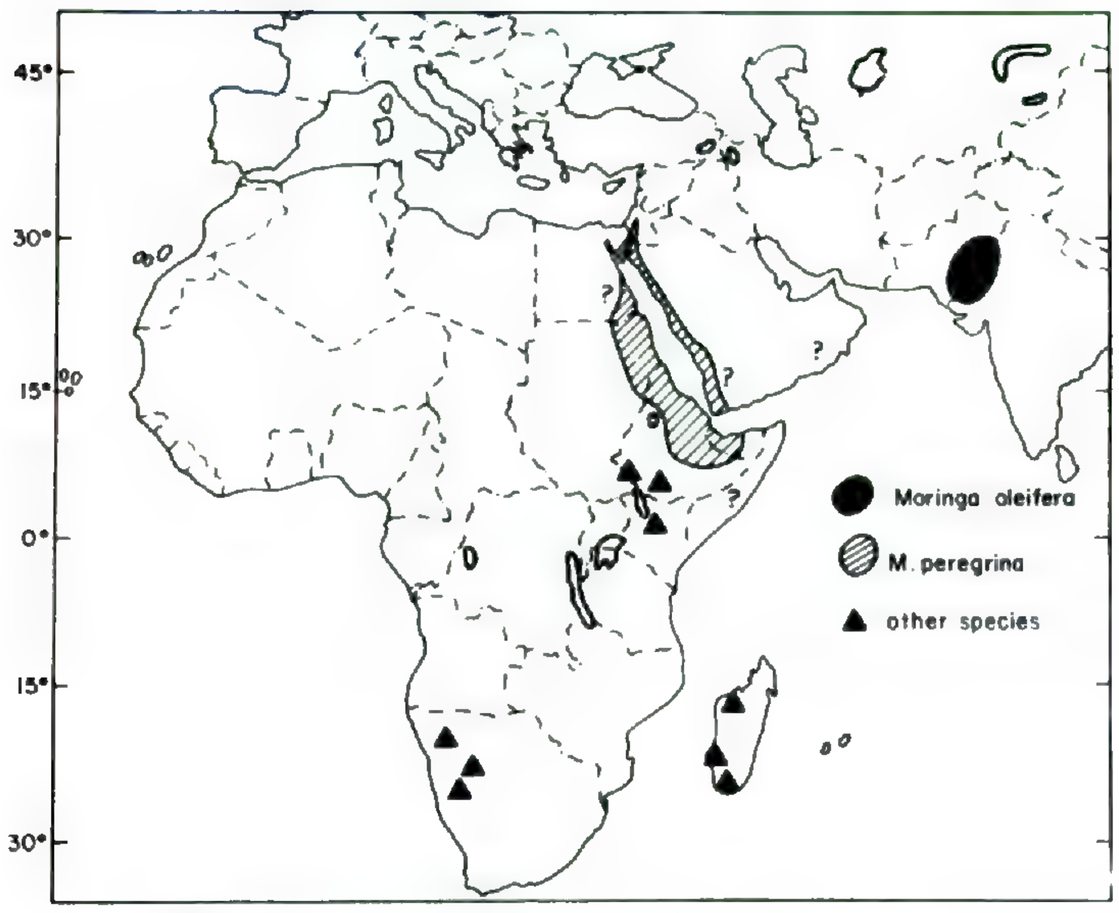

FIGURE 10. Distribution map of some *Moringa* spp. (after Kerauden, 1965).

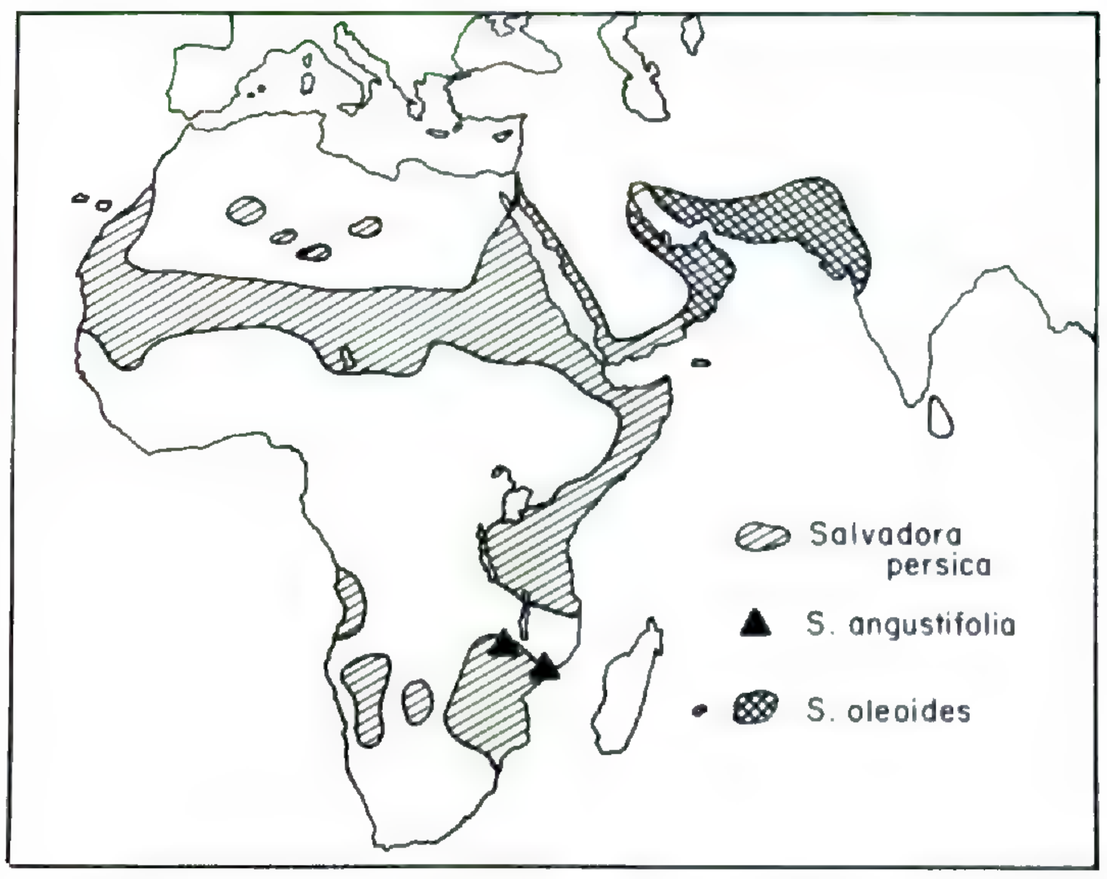

FIGURE 12. Distribution map of some *Salvadora* spp.

are probably accomplished with the aid of physiological-biochemical adaptations of new populations to lower and lower temperatures.

Other examples of savanna grasses turned ruderal include *Desmostachya bipinnata* and *Aristida sieberiana.* As was mentioned with respect to *Ziziphus spina-christi,* so again in the grasses, a certain transitional character must be examined. Within the Rift Valley most of these grasses occur strictly in moist habitats, salt marshes, or rocky outcrops—or more recently, as weeds in plowed fields and along roadsides. In the warm, moist parts of the coastal plain, where they occur in far fewer numbers, they are found in disturbed sites. However, in some cases they also appear to be well integrated in the oak woodland association, as will be discussed below.

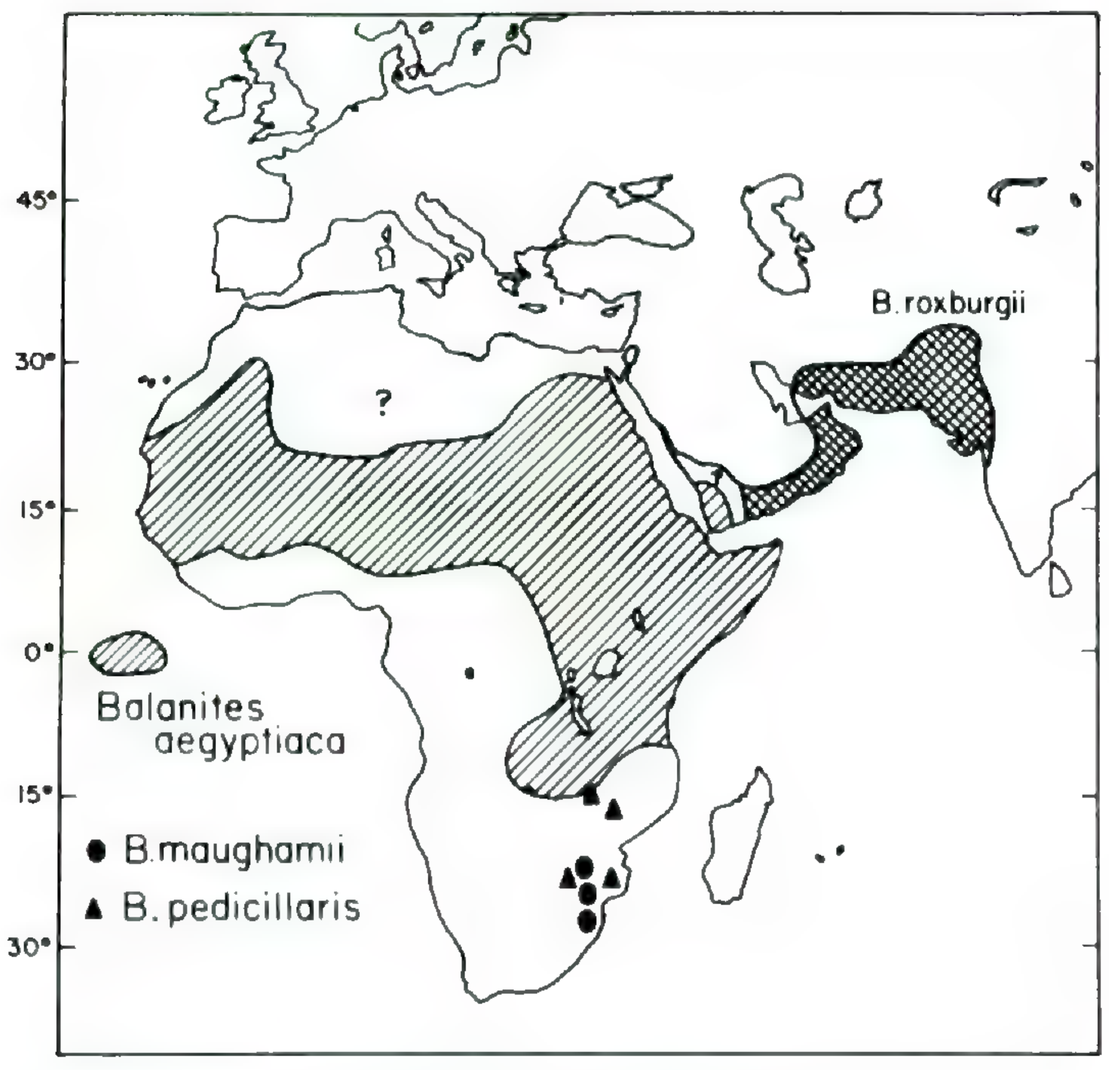

FIGURE 11. Distribution map of some *Balanites* spp. (with the assistance of M. J. S. Sands).

AQUATICS AND HYDROPHILES

A second group of Sudanian elements found mainly outside the Sudanian enclave of the Rift are hydrophilic species. Some of these grow in swamps or other perennially aquatic habitats (e.g., *Cyperus jeminicus, Nymphaea alba,* and *Vigna luteola*). Others grow in moist recesses from which they have migrated to cultivated fields (e.g., *Chrozophora tinctoria, C. plicata,* and *Commicarpus africanus*). Those areas of primary wet habitats in which the water level and channels can change rapidly and unpredictably are populated in part by species pre-adapted to secondary habitats such as roadsides and cultivated fields.

FULLY INTEGRATED SUDANIAN ELEMENTS

Desmostachya bipinnata is an important Sudanian grass that grows in a variety of soils in the east African savannas (Wickens, pers. comm.) and in the Thar Desert (Bhandari, 1978). In the Arava it is dominant in salt marsh and saline sand communities. Along the coastal plain it occurs in the natural oak woodland community of *Quercus ithaburensis* on red sandy loam (Eig, 1946; Zohary, 1955). This thermophilic plant community also includes additional Sudanian components such as *Aristida sieberiana, Stipagrostis obtusifolia,* and *Ziziphus spina-christi.* The *Quercus ithaburensis–Desmostachya bipinnata* association is part of a broad transitional trend

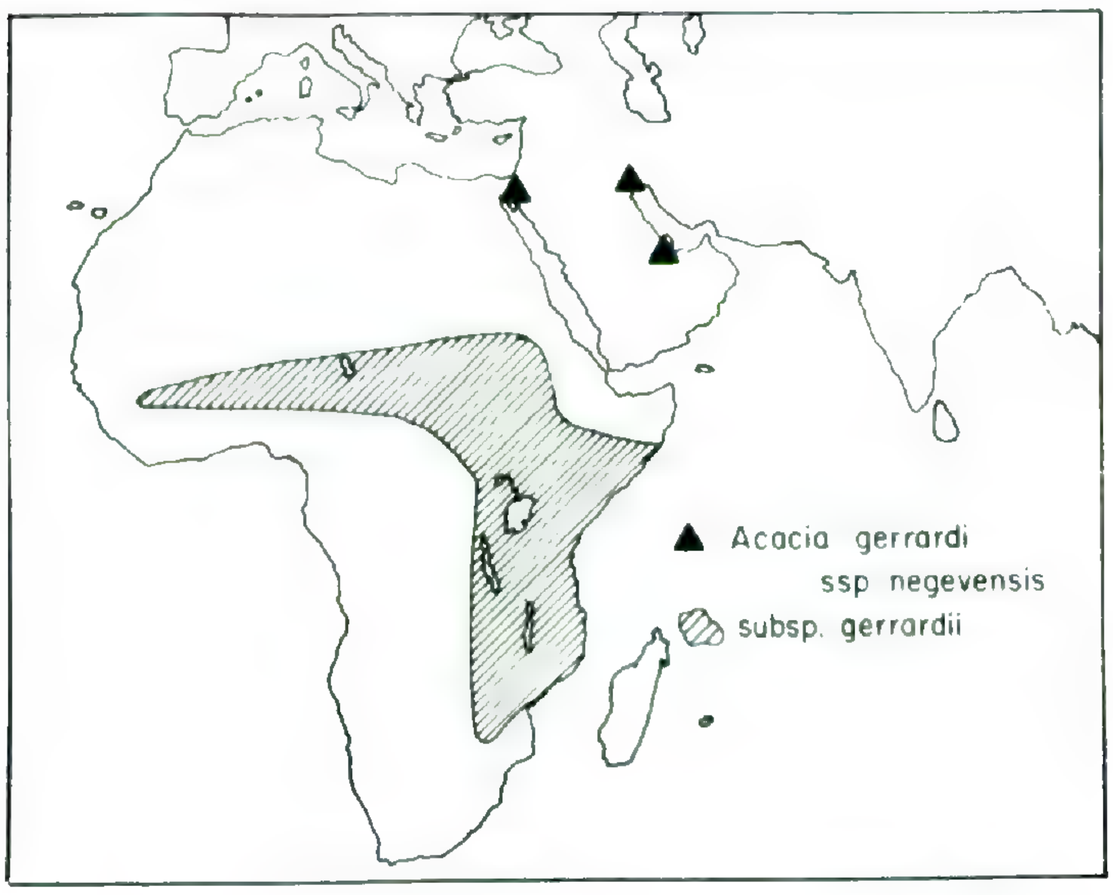

FIGURE 13. Distribution of *Acacia gerrardii* subsp. *negevensis* and subsp. *gerrardii* (after Halevy, 1971; Ross, 1966; Wickens, pers. comm.).

from the holarctic to the tropical regions. A similar transition gradient occurs in North America, where northern oaks, along with tropical *Prosopis* and Poaceae constitute the "savanna" vegetation in parts of southern Texas and southern Arizona (Whittaker et al., 1979). In this oak woodland community of the coastal plain is found the only recorded endemic Sudanian species in Israel occurring entirely outside the Dead Sea Rift—*Aristida sieberiana*. The genetic-systematic relatives of this grass species are not clear, and considerable controversy exists on the endemic status of this taxon (Feinbrun, pers. comm.). Further studies may alter its current status.

As mentioned above, both *Ziziphus spina-christi* and some of the grasses belong both to the ruderal group and to the group of fully-integrated species. In fact a *Ziziphus spina-christi–Hyparrhenia hirta* community is recognized along the coastal plain. Zohary (pers. comm.) assumed that the climax area of this community occurred in the southern portion of the coastal plain. Due to intensive cultivation and woodcutting, however, not many locations remain that can still testify to this presumed climax vegetation. In the northern portion of the coastal plain, it is replaced by the *Ceratonia siliqua–Pistacia lentiscus* community that dominates the coastal foothills. Even in this community where most of the components are typical Mediterranean, the dominant species show a strong Sudanian affinity. For example, *Ceratonia siliqua* grows wild in the mountains of Yemen and clearly belongs to a tropical section within its family. Only recently, a new species of *Ceratonia*—*C. oreothauma* was discovered in isolated, disjunct regions of Arabia and Somalia providing further indication of a tropical origin for this genus (Hillcoat et al., 1980). *Pistacia lentiscus* is also reported from the colline regions of east Africa (Lind & Morrison, 1974; Zohary, pers. comm.). At present, the principal distribution of both these species is in the colline belt around the Mediterranean Sea. Yet they exhibit both systematic and ecological (they are both evergreen sclerophyllous and thermophilic) links to the Sudanian tropical vegetation. Because the links are usually evident only at the generic level, Zohary (1955, 1973) assumed that they were very ancient links going back as far as the Miocene, when tropical vegetation dominated the entire Mediterranean region and central Europe.

ANOMALOUS GROUP

In addition to the three groups described above, two additional species should be mentioned that conform to none of the above patterns and theories. The first of these is *Acacia gerrardii* subsp. *negevensis*. The map in Figure 13 shows the distribution of *Acacia gerrardii* with geographical delineation of the two recognized subspecies. The generic distribution pattern reveals a remarkable degree of disjunction between subspecies *negevensis* in southern Israel and a few sites in southwestern Arabia and the more widespread subspecies *gerrardii* in eastern and southern Africa. Moreover, *A. gerrardii* subsp. *negevensis* does not occur, in Israel at least, in typical Sudanian conditions (Halevy, 1970). Instead of occupying wadi beds in the Arava Valley, such as are preferred by *Acacia tortilis* and *A. raddiana*, this subspecies grows in only a few adjacent watersheds in the highlands of the southern Negev and one or two sites in eastern Sinai. It appears to be adapted to cool habitats, which represents an ecological shift from its primary warm habitats, as seen in Africa. Its restricted geographical area and lack of penetration to adjacent cool, open areas (e.g., the Mt. Ramon Range and the Sante Katerina Highlands in Sinai) are indicative of an extreme relict position in the area. Further evidence for this view is provided by the anomalously disjunct pattern (southern Negev, eastern Sinai, Kuwait), which is unlike that of any other Sudanian species. Significantly, *A. gerrardii* subsp. *gerrardii* is also a watershed species throughout its range in Africa (see Fig. 13, Wick-

ens, pers. comm.). Finally, it is worth noting that the Jordan Sparrow, *Passer moabiticus,* exhibits a similar disjunct pattern, occurring only in Israel, Jordan, and the Persian Gulf region (Boros & Horvath, 1954; Kumerlove, 1971).

The second anomalous species is *Acacia albida* (= *Faidherbia albida*), which occurs in a few isolated sites of the Mediterranean coastal plain, a few sites in the Jordan Valley north of the Dead Sea, and one or two isolated spots elsewhere in the country (Halevy, 1971). It does not occur in the Negev or Arava Valley (Aaronsohn, 1913; Karschon, 1961; Aloni & Orshan, 1972; see Fig. 14). Unlike its typical ecological patterns in Africa (Radwanski & Wickens, 1967; Wickens, 1969; Ross, 1966, 1979, 1981), it is not restricted to riparian or high ground-water sites in Israel. It also differs in that flowering and fruiting are relatively rare in all the sites at which it occurs in Israel, while vegetative propagation by suckers is far more common (Halevy & Orshan, 1972). Zohary (1962) has argued for the relict position of this species in Israel; indeed, the anomalous position of *A. albida* within the genus *Acacia,* and its occurrence with typical Mediterranean associations such as *Artemisia monosperma* and *Cyperus mucronatus* along the coastal plain, support that conclusion. However, the overall distribution pattern of the species in Israel (Fig. 14) and its atypical ecological characters here, could instead indicate a recent arrival and penetration to this area from the Nile River Basin rather than along the Syrio-Africa Rift.

Throughout Africa *Acacia albida* exhibits a phenological feature unusual to but not unique among savanna trees in that it sheds its leaves at the beginning of both rainy seasons (Wickens, 1969; Pelissier, 1977). In Israel, bi-annual shedding of the leaves occurs although there is only one rainy season per year. In the case of an ancient relict, we would expect this character to have been modified rather than preserved. Moreover, recent investigations on the northernmost branch of the Nile River indicate that as recently as the sixth century A.D. this so-called Pelusiac branch was active and extended a considerable distance into the northern Sinai Peninsula (Sneh & Weissbrod, 1973). It does not seem impossible, therefore, that *Acacia albida* should have been gradually dispersed by one or more vectors along the Mediterranean coast and finally to the Jezreel Valley and Beit Shean on the one side and as far north as southern Lebanon on the other (Halevy, 1971).

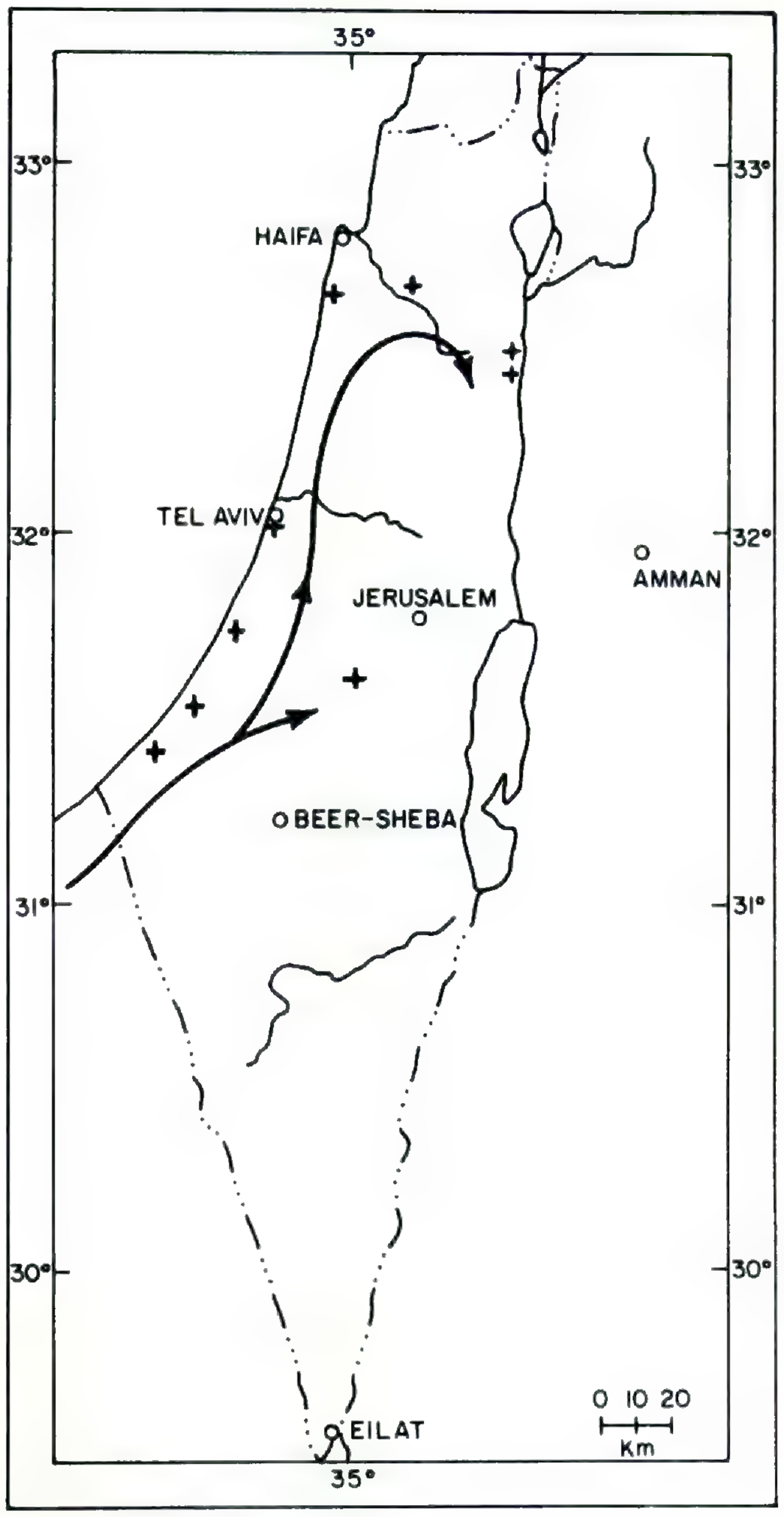

FIGURE 14. Distribution of *Acacia albida* in Israel. The arrows indicate the presumed penetration route (after Halevy, 1971).

ADAPTATION OF SUDANIAN SPECIES TO ARIDITY AND LONG-RANGE DISPERSAL

Regardless of the age of the Sudanian elements found in Israel today the question naturally arises: how and why did some elements arrive (and remain) here and not others? Given that the Dead Sea Rift and the other regions in Israel in which Sudanian elements are found do not enjoy the same amounts of rain that fall in the Sudanian region proper, and that what rain does occur is concentrated in only one rainy season, it might be supposed that various adaptations or pre-adaptations to drought would be found in the Sudanian elements in Israel. Obviously, it is difficult or impossible to analyze such factors

TABLE 5. Dispersal analysis of the Sudanian arboreal floras of Sudan, Egypt, and Israel (see text for details).

Long-distance Dispersal Vector	Sudan[a,d]		Egypt[b,d]		Israel[c]	
	Number	Percent	Number	Percent	Number	Percent
Wind	56	14.0	11	8.5	9	18.4
Endozoochory	189	47.25	73	56.1	22	44.9
Exozoochory	2	0.5	8	6.2	4	8.1
None apparent	153	38.25	38	29.2	14	28.6
Total	400	100.0	130	100.0	49	100.0

[a] Species list drawn from Andrews (1950–1956) and modified after Wickens (1968).
[b] Species list drawn from Täckholm (1974) with modifications.
[c] Species list drawn from Zohary and Feinbrun-Dothan (1966–1974), Feinbrun-Dothan (1978, 1985), and personal observations of the authors. Full species list with information on growth form, flowering period, chorotype, dispersal unit, and presumed dispersal vector is available from A. Shmida.
[d] Full species list with details of growth forms and presumed dispersal systems is available from the authors.

quantitatively, short of in situ field comparisons of the same species occurring in Sudan, for example, and in Israel.

On the other hand, a partial analysis of adaptations for long-distance dispersal of seeds is possible, on the basis of personal observations and study of the published floras of Israel, Egypt, and Sudan. Anemochory and zoochory would clearly facilitate more efficient dispersal of Sudanian elements to the Dead Sea Rift Valley and enable dispersal units or diaspores to reach the rare and disjunct habitats within the Rift that are suitable to their requirements. Members of the Asclepiadaceae (e.g., *Calotropis, Periploca, Leptadenia,* and *Solenostemma*) have a pseudopappus attached to each seed, which is clearly important in long-distance dispersal. Certain grasses (e.g., *Pennisetum, Tetrapogon,* and *Trichodiaena*), Geraniaceae, *Monsonia* spp., and *Abutilon* spp. have dispersal mechanisms very similar to those of the Asclepiadaceae.

Yet another ecological group with efficient long-distance dispersal mechanisms is the endozoochorous species, whose dispersal units are juicy berries eaten by birds (e.g., *Maerua, Ephedra, Lycium,* and *Salvadora*) or larger diaspores eaten by mammals and other large animals (e.g., *Acacia, Balanites, Cordia,* and *Ziziphus*). However, many Sudanian species in Israel lack any apparent long-distance dispersal mechanism.

Table 5 shows a comparison of the relative importance of the major long-distance dispersal vectors of seeds, anemochory and zoochory of trees, shrubs, and perennial vines in the Sudanian elements of Israel, Egypt, and Sudan excluding Equatoria Province. This analysis unavoidably relies to a certain extent on speculation; however, in all cases where no readily apparent morphological adaptation for long-distance dispersal was discernible, none was assumed. The flora of Sudan was chosen as the basis for comparison to Israel, since a fairly reliable flora was published rather recently (Andrews, 1950–1956) and considerable systematic work has been conducted in Sudan since then (cf. Wickens, 1968, 1977). All species occurring in the mountainous regions and Equatoria Province of Sudan, which are characterized by a moist tropical climate, were excluded from the analysis. The remaining portions of Sudan—the savannas, semidesert, and Red Sea Hills—were considered representative of the Sudanian phytogeographic region. Certainly, a west African region should have been compared as well, but we were unable to find a suitable flora.

In addition, the Sudanian elements of the arboreal flora of Egypt (Täckholm, 1974) were analyzed as a kind of mid-way station between Sudan and Israel. Finally, the Sudanian arboreal elements in Israel were analyzed in somewhat more detail; in almost all cases, the geographical ranges (chorotypes) were accepted as given by Zohary and Feinbrun-Dothan (1966–1974) and Feinbrun-Dothan (1978, 1985).

We concentrate only on the arboreal elements in each of the three countries for two main reasons: 1) the dispersal spectra and taxonomy of the non-arboreal floras of Egypt and Sudan are less well-known; and 2) the arboreal floras of Egypt and Israel are presumed to give the best picture of the "permanent" Sudanian elements to be found there. We have excluded arboreal elements characterized by Irano-Turanian or other non-Sudanian chorotypes e.g., *Pistacia,*

TABLE 6. Habitat shifts of some Sudanian elements in different geographical areas.

Name	Sudan	Dead Sea Rift Valley	Outside Dead Sea Rift Valley, esp. Coastal Plain
Trees			
Acacia albida	high ground water or flood plains (habitat)	—	a variety of diversified habitats—sands, basaltic slopes, and dry wadi beds
Acacia gerrardii ssp. *gerrardii*	flood plains	wadibeds in extreme cold desert	—
Balanites aegyptiaca	scattered trees in savanna	oases and rocky cliffs	—
Moringa peregrina	Red Sea Hills; savanna	oases and rocky cliffs	—
Ziziphus spina-christi	scattered trees in savanna	oases and moist wadi beds	ruderal, segetal
Halophytes			
Desmostachya bipinnata	savanna grass	saline sinks	oak woodland
Hyphaene thebaica	sparse in savanna	saline marshes	—
Phoenix dactylifera	introduced; naturalized	oases and saline marshes	—
Vines			
Cocculus pendulus	climbers in savanna	cliffs	—
Ephedra foliata	climbers or shrubs	shrubs	aggressive climber on cultivated trees
Pentatropis spiralis	slender climber in savanna	fleshy climber in saline sink	—
Pergularia tomentosa	small shrub	small shrub or climber	small shrub
Grasses			
Pennisetum setaceum	savanna	rocky cliffs	ruderal
Trichlolaena teneriffae	sparse in savanna	rocky cliffs	recently invading roadsides in patches
Aristida sieberiana	dry savanna	rocky cliffs	south-facing rocks
Tetrapogon villosus	dry savanna	crevices in rocky cliffs	—

Juniperus, Colutea, Calligonum, and *Haloxylon.* Introduced and cultivated species were excluded as well, for example, *Ficus sycamorus* in Israel, and *Moringa oleifera, Dalbergia sissoo,* and *Lawsonia inermis* throughout. Such a comparison does not reveal a clear indication that the Sudanian elements in Israel show a higher proportion of species with adaptations for long-distance dispersal than those in Egypt or Sudan, although a somewhat higher percentage of Sudanian elements in Israel has adaptations for wind dispersal and exozoochory. The most striking result is that the arboreal Sudanian floras in all three areas show a very high percentage of long-distance dispersal adaptations (61.75, 70.8, and 71.4% in Sudan, Egypt, and Israel, respectively).

On the basis of this analysis we conclude that adaptations for long-distance dispersal do not provide a clue as to the question of the age of the Sudanian flora in Israel. However, they certainly play an important role in the dispersal and survival of those elements in Israel and elsewhere in their geographical ranges.

DISCUSSION

The Sudanian assemblage of plants in Israel exhibits a typical example of the evolutionary and ecological processes that can take place in a locus terminus, where populations are small, disjunct, and vulnerable to extinction. In short, such populations face ecological and environmental conditions quite different from those in their central distribution area in Africa (Fig. 1). In the following paragraphs, we summarize the distinctive features that characterize the Sudanian elements in Israel.

ENVIRONMENTAL CONDITIONS

The environmental conditions in which the Sudanian elements occur in Israel are generally similar to those in the main Sudanian dominion in Africa. However, there are some critical differences: in Israel there is a greater contrast between winter and summer conditions, and the overall yearly precipitation is less predictable. Moreover, the rainfall patterns are completely different. In the Sudanian region of east Africa there are two principle rainy seasons—autumn (October–November) and spring (March–April) (Lind & Morrison, 1974), but in Israel virtually all of the rain comes in the winter (December–March) (see Fig. 10).

GEOGRAPHICAL AND ECOLOGICAL SPLITTING OF THE SUDANIAN ELEMENTS

The Sudanian elements penetrating Israel from the south split and inhabited two distinct habitats when they reached the Dead Sea Rift Valley: arboreal elements that grow in large wadis and grasses and other smaller lifeforms that tend to grow in the thermic micro-environments occurring among open rock formations.

Both a splitting of the natural Sudanian association and an intermingling of the Sudanian elements with the Saharo-Arabian and Mediterranean floras have occurred. In most places, even in the most typical "Sudanian habitats" in Israel, the Sudanian elements constitute only a small percentage of species present and are interspersed among the eremaic flora. Zohary (1962, 1973, 1982) devoted a special geographical district to the Sudanian elements in the Arava Valley and Dead Sea area, but phytogeographical analysis of the community shows that the Sudanian elements account for less than 15% of the total species list (see section on Distribution Patterns below). Accordingly, Feinbrun-Dothan (1985) does not recognize a Sudanian phytogeographic territory in the "Flora Palaestina." As mentioned earlier, we heartily concur with this view.

HABITAT SHIFT AMONG THE SUDANIAN ELEMENTS

Habitat shift is a phenomenon consisting of definite changes in the environmental parameters of the niche space occupied by a given species in comparison to the parameters of the niche space in another portion of the species' geographical range (MacArthur, 1968, 1972; Pianka, 1978; Diamond, 1975). Such patterns have been frequently found in zoology (Diamond, 1975; Pianka, 1975; Krebs & Davies, 1978) but are almost completely unnoticed in botany (see Cody & Mooney, 1978).

Our study reveals cases of habitat shift on two geographical scales: a) the east African savannas and the Arterial Desert savannas of the Dead Sea Rift; and 2) the Dead Sea Rift and the coastal plain. Table 6 summarizes the most obvious habitat shifts displayed by the Sudanian elements under study. Most of the habitat shifts can be at least partially explained by the Eco-Geographical Rule of Boyko (1947). Since the plants in Africa are accustomed to a fairly high regime of rainfall, where they penetrate into the arid parts of Israel, they tend to be confined to habitats with improved water regimes relative to the surrounding area. Nevertheless, these specialized habitats have components that differ markedly from the African savannas even if the amount of water is approximately the same. In saline habitats, for example, the plants must contend with a high concentration of salts, whereas in rocky habitats they face a high degree of unpredictability in their water supply.

Another major habitat shift occurs in the coastal plain, where most of the Sudanian species occupy ruderal and especially segetal sites. As the cultivation of summer crops has expanded in the area over the past 100 years, certain Sudanian elements have exhibited a remarkable preadaptation to disturbed sites with artificially supplemented water in the summertime (Dafni, 1975). Some of these have become aggressive weeds throughout the coastal plain (e.g., *Chrozophora tinctoria*; see Table 5). Yet another case of habitat shift is displayed by those Sudanian vines that are typically climbers but in the Dead Sea Rift are restricted to cliffs and only seldomly occur on trees (e.g., *Cocculus pendulus*). We propose that some of the cucurbits have also undergone a habitat shift, wherein typical savanna climbers became prostrate spreading vines in the arterial wadi beds (e.g., *Cucumis prophetarum, Citrullus colycynthis*), but in this case the shift apparently took place at the genus level, relatively early in the evolution of the relevant sections of the family. A similar trend occurs in the *Commicarpus/Boerhavia* complex, in which some are climbers, some are facultative climbers (*Commicarpus africanus*), and some are exclusively prostrate wadi-bed vines (e.g., *Commicarpus boissieri*). This trend seems to represent

a general pattern of shift of growth form concomitant with a migration from semi-desert savanna environments to extreme desert habitats.

ASSOCIATION AND RE-ARRANGEMENT

In general terms, in comparing the association of Sudanian elements in Israel with the entire association of the Sudanian flora in Africa, we find a complete lack of agreement between them. The main differences are that in Israel the Sudanian elements occur together with many species of other chorotypes and that even the details of their co-occurrence are different from those found in Africa. This pattern of non-consistent association corresponds to Gleason's (1926) individualist concept of plant geography and phytosociology, an approach that was quantitatively developed and substantiated by Whittaker (1962). Nevertheless, a small "core group" of taxa can be distinguished that are, in Israel, restricted to the Dead Sea Rift Valley. We shall call this the *Arava Group* (a). They are all species universally recognized as belonging to the basic Sudanian flora, which occurs continuously, if disjunctively, from dry tropical Africa to the Thar Desert. *Salvadora persica, Balanites aegyptiaca, Calotropis procera,* and *Acacia tortilis* are good examples of this group (see Figs. 4, 11).

A second group is the *Fully Integrated Group* (b). These are paleo-Mediterranean elements (sensu Zohary, 1973) that do not have phylogenetic allies among temperate floras but instead good, if remote, systematic links to the tropical flora. They comprise several species endemic to the Mediterranean region that currently do not occur in tropical or Sudanian regions but are replaced there by a congeneric relative (e.g., *Olea europaea* replaced by *O. chrysophylla, = O. europaea* subsp. *africana*) or by related genera within the same familial section or tribe (e.g., *Laurus, Nerium, Phillyrea,* and *Tamus* vis-à-vis their tropical counterparts). Zohary (1973) postulated that this group has survived since the Miocene around the Mediterranean Basin while most of the tropical elements occurring with them at that time retreated to the warmer regions of Africa (and Asia).

The *Transitional Group* (c) includes those species that grow in both the Dead Sea Rift and in the Mediterranean region of Israel, e.g., *Ziziphus spina-christi, Demostachy bipinnata,* and *Hyparrhenia hirta.* These species are characterized by differences in habitat in the two areas, as described earlier. In the Dead Sea Rift, they are restricted to moist habitats, i.e., salt marshes or rocky outcrops; and in the Mediterranean region, most of them are relatively widespread, especially in warm and at least slightly disturbed habitats. Indirect and published literary evidence suggests extensive invasion and expansion of these elements throughout the Mediterranean region within the last century. Yet it seems clear that the primary distribution of these species, including the now weedy grasses, is Sudanian (Eig, 1938; Zohary, 1973). For this reason we recognize them as a separate group.

In addition to the three groups described above an *Anomalous Group* (d) can be recognized, which includes *Acacia albida* and *A. gerrardii* subsp. *negevensis.* As described earlier, these two species show complex distributional and ecological patterns in Israel, the elucidation of which will require further study of the geological and paleoecological past of the area.

RARITY, DISJUNCT DISTRIBUTION PATTERNS, AND THEIR ECOLOGICAL CONSEQUENCES

Habitats in Israel where Sudanian plants dominate (Fig. 9)—rocks, cliffs, oases, and large wadis—are scattered in a topographical matrix of desert slopes that do not permit the existence of non-xeric plants. Consequently, most populations of these Sudanian species in Israel are small and disjunct.

In many rocky habitats in the Dead Sea area and along the Arava Valley, common desert species (Saharo-Arabian elements) are found instead of Sudanian species. The absence of Sudanian elements in these apparently suitable sites is probably due to high rates of local extinction (cf. Stebbins, 1952) and rare recolonization events.

THE AGE OF THE SUDANIAN ELEMENTS IN THE FLORA OF ISRAEL

Points in favor of the antiquity of Sudanian vegetation in the study area are the following:

1. Strong paleontological evidence exists for the gradual decrease (attenuation) of tropical animals in the area from the Miocene to the Holocene (Tchernov, 1968, 1975).
2. The "paleomediterranean elements" (sensu Zohary, 1973) of Israel show a distinctly relict distribution pattern with secondary adaptations to the Mediterranean area. Examples are

Olea europaea and *Ceratonia siliqua,* both of which are present-day components of the evergreen maquis that have decidedly tropical affinities.

3. The random and disjunct character of many Sudanian species growing in oases and by springs in cliffs and gorges might suggest that the vegetation is relict in character (Zohary, 1962, 1973). According to this theory, the vegetation that once covered the whole area contracted to moister habitats as the climate grew dryer.

Points in favor of the recency of most of the Sudanian vegetation in the study area are:

1. Cold conditions in the Pliocene and the glacial periods of the Pleistocene were unfavorable to Sudanian vegetation existing in the study area, which was consequently destroyed after the Miocene (Galil, 1972).
2. Up to the Pleistocene the Dead Sea Rift was apparently only a shallow depression, in which a pseudo-Sudanian climate appropriate for thermophilic Sudanian species could not exist. During the last glacial period the central Dead Sea Valley was covered by the Lisan Lake and the climate was cooler (Neev & Emory, 1967; Horowitz, 1979) and therefore not appropriate for the existence of the xerophytic Sudanian species growing there today.
3. Most Sudanian species in Israel have undergone virtually no speciation relative to their larger populations in east Africa. Those taxa that have speciated have done so to a very low degree (variety or subspecies level). In most species with endemic taxa, gradual morphological transitions can be found between the endemic taxa and the corresponding Sudanian sibling species.
4. Many Sudanian species have efficient long-distance dispersal mechanisms and could have reached the disjunct habitats suitable for their growth by this method (see previous section on Long-Range Dispersal). In light of recent research on the seed dispersal ability of many plants occurring on oceanic islands (Carlquist, 1974), this evidence seems significant.
5. The disjunct and apparently random distribution of Sudanian vegetation in the Dead Sea Rift can be attributed not only to their being relicts from a different climatic period, but also to long-distance dispersal and the scarcity of appropriate habitats. According to this view, many habitats suitable for the existence of Sudanian vegetation can be expected to remain empty or populated by only one species (cf. Ellner & Shmida, 1981). What seems to be a random pattern at the single species level can be explained by consistent statistical evidence at the community and total Sudanian flora level (see Ellner & Shmida, 1981).
6. That the indisputably relict "paleomediterranean elements" occur entirely in the Mediterranean region of Israel and not in the Dead Sea Rift is further evidence that relicts and recent arrivals show divergent distribution patterns in the study area. The unique distribution of *Acacia gerrardi* subsp. *negevensis* also stands in marked contrast to that of the remainder of the Sudanian elements in the area. The former shows a clearly relict pattern while the latter do not.
7. The existence of a transitional group and a wide range of marked habitat shifts (see previous sections) in the Sudanian elements occurring in Israel outside of the Dead Sea Rift also argues for the recency of the Sudanian flora as a whole in the area. Invasion and penetration of these elements can be seen taking place at a rapid rate in localities characterized by human disturbance.
8. Very few endemic species are found in the Dead Sea Rift where the great majority of Sudanian floral and faunal elements in Israel occur. The only clear exceptions are the boraginaceous chamaephyte *Trichodesma boissieri* and the sunbird, *Cinnyris osea,* both of whose nearest systematic relatives occur in east Africa, over 1,000 km away. In the Mediterranean region, one paleoendemic Sudanian butterfly exists, namely *Caharexes jasius* (Larsen, 1974). By contrast, in both the Irano-Turanian and the Mediterranean elements of the Israeli flora, a large number of endemics or sub-endemics exist. Many of these occupy rocky or otherwise locally isolated habitats. Similar habitats supporting Sudanian elements, although many hundreds of kilometers away from their nearest congeneric neighbors, are nevertheless devoid of paleoendemics.

CONCLUSIONS

In our opinion, the large majority of the Sudanian plant species occurring in the Negev and

Dead Sea Rift Valley today are of recent origin and have reached the area only after the last glacial period. That is, most of the Sudanian species presently occurring in Israel, with the exception of *Trichodesma boissieri* and *Acacia gerrardi* subsp. *negevensis,* started to penetrate from the south about 12,000 to 17,000 years ago. This process continued throughout the Holocene. This conclusion does not exclude the possibility that Sudanian elements, including some of the same species found here today, existed in Israel in more ancient times during the Pleistocene and late Tertiary. Nevertheless, the existence of Tertiary tropical flora in Israel has yet to be proved by fossils. By contrast, evidence for tropical fauna during the early Pleistocene is plentiful, mainly from the fossils found at Ubediyah of the elephant, giraffe, and hippopotamus (Tchernov, 1975; Bar Yosef & Tchernov, 1972).

It is interesting to note that analogous questions concerning the age of a northern tongue of penetration of the Mediterranean *Arbutus* group were investigated by Sealy (1949). The occurrence of *Arbutus unedo* in habitats edaphically unsuitable for woodland in a few sites in Brittany and western Ireland, surrounded by plants of very different overall chorotypes, was investigated from a variety of angles. Rejecting the argument of an ancient relict situation for this Mediterranean element far from its main phytogeographical region, Sealy concluded that *Arbutus unedo* had invaded these isolated habitats only recently, for reasons very similar to those favored by us concerning the Sudanian elements in Israel.

Kosswing (1955) analyzed the biogeography of tropical elements in Turkey and concluded that some of the Sudanian elements are ancient (20 million years or more) while others are recent (hundreds of thousands of years). The same is true of the Sudanian elements in Israel, according to the opinion held by most biogeographers in Israel today (Galil, 1972; Heller, pers. comm.; Lipkin, pers. comm.; Tchernov, pers. comm.). The question now is the size and importance of the patterns, speciation level, and phylogenetic relationships of Sudanian vegetation. We conclude that in the Negev and Dead Sea Rift Valley the overwhelming majority of Sudanian elements are very recent. They penetrated the area primarily along the Syrian-African Rift during the various inter-glacial periods. Most of the extant Sudanian vegetation probably reached the area only at the end of the upper Pleistocene and during the Holocene, after the Lisan Lake dried up and the rapid deepening of the Rift took place. On the other hand, a significant portion of the species with tropical affinities occurring in the Mediterranean area of Israel are probably ancient and can be considered Miocene relicts, both from their geographical disjunction and systematic isolation (Zohary, 1973).

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SYSTEMATIC FOLIAR MORPHOLOGY OF PHYLLANTHOIDEAE (EUPHORBIACEAE). I. CONSPECTUS[1]

GEOFFREY A. LEVIN[2]

ABSTRACT

Leaf architecture and epidermal morphology of 259 species representing 51 genera in the Phyllanthoideae (Euphorbiaceae) vary in a taxonomically significant way. Most tribes are relatively homogeneous and well defined, with most exceptions being tribes containing herbaceous or highly xerophytic genera. Tribes that are generally considered to be closely related have similar leaves. Increase in venational organization correlates with specialization in floral morphology. Foliar morphology also indicates genera whose relationships warrant reconsideration, particularly *Celianella, Croizatia, Didymocistus, Jablonskia, Neowawraea,* and *Uapaca.* Theoid teeth and incipient or vestigial actinodromy support placement of Euphorbiaceae near the Violales in the Dilleniidae, rather than in the Rosidae.

Paleobotanists, faced with the task of identifying fossil angiosperms in the absence of megafossils of reproductive parts, have instead depended on the morphology and anatomy of vegetative structures, especially leaves. The last three decades have seen a tremendous increase in the sophistication of the techniques for investigation and description of foliar morphology (review by Dilcher, 1974; see also Fryns-Claessens & van Cotthem, 1973; Hickey, 1973; Hill, 1980; Payne, 1979; Stace, 1965). Particularly important in this progress was Hickey's (1973) development of a precise and non-overlapping terminology for the description of dicotyledonous leaf architecture, defined by Hickey as "the placement and form of those elements constituting the outward expression of leaf structure, including venation patterns, marginal configuration, leaf shape, and gland position."

Taxonomists studying higher taxa of extant angiosperms have generally ignored foliar characters, particularly aspects of architecture. Yet Hickey and Wolfe (1975), in their pioneering survey of dicotyledon leaves, found "coherent patterns of morphology of apparent value in determining taxonomic and phylogenetic relationships" at the ordinal and subclass levels. A few other studies have demonstrated higher systematic value in leaf architecture, notably in the Hamamelididae (Wolfe, 1973), Onagraceae (Hickey, 1980), Marcgraviaceae (Bedell, 1981), Rubiaceae (Pray, 1953), and Rutaceae (Dede, 1962). Clearly, however, the leaf architecture of extant angiosperms remains largely unexplored by systematists.

Cuticular characters have had a longer history of use in taxonomic investigations (see review by Stace, 1965), although here, too, our knowledge of fossil cuticle may exceed what we know of extant angiosperms. Epidermal features have proven systematically useful in several dicotyledonous families, including, among others, the Celastraceae (Den Hartog & Baas, 1978), Euphorbiaceae (Raju & Rao, 1977), and Magnoliaceae and related families (Baranova, 1972).

The Euphorbiaceae are an ideal family with which to explore the potential contribution of leaf architecture and epidermal morphology to higher level taxonomy. This large family, which contains about 300 genera and 7,000 species (Webster, 1967), has long attracted systematists' attention, resulting in an impressive series of infrafamilial classifications. The first treatment, by Jussieu (1824), has been succeeded by further treatments prepared by Baillon (1858), Mueller (1866), Bentham (1880), Pax (1890), Pax and Hoffmann (1931), Hurusawa (1954), and Hutchinson (1969). In addition to the information on floral morphology on which these systems are largely based, evidence has accumulated on anat-

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omy (Rothdauscher, 1896; Gaucher, 1902; Pax & Hoffman, 1931; Metcalfe & Chalk, 1950: 1207–1235; Hayden, 1980), palynology (Erdtman, 1952: 165–175; Punt, 1962; Köhler, 1965), and cytology (Webster & Ellis, 1962; Miller & Webster, 1966). Webster (1975) produced a treatment taking into account data from all these fields. Yet, in spite of all this attention, the foliar morphology of the Euphorbiaceae remains little known (but see Sehgal & Paliwal, 1974; Hayden, 1980).

The phylogenetic relationships of the Euphorbiaceae are controversial, which also makes the study of euphorbiaceous leaf architecture potentially valuable. There are two schools of thought regarding the position of the family. The first has accepted rosid affinities. Based on the pluriloc-ular gynoecium containing two (or one) ovules in each locule and the presence of a nectary disk, Cronquist (1981) argued for a close relationship to the Celastrales. Webster (1967) was much more cautious, suggesting that Euphorbiaceae evolved from a primitive rosalean plexus. Among living orders, he considered the Euphorbiaceae closest to the Geraniales, with which they share a similar gynoecium and epitropous ovules. The second school has placed the Euphorbiaceae in the Dilleniidae near the Violales and Malvales (Croizat, 1940; Hickey & Wolfe, 1975; Takhtajan, 1980; Thorne, 1976). These authors emphasized the similarities between the wood, leaves, gynoecium, and pollen of the Euphorbiaceae and the primitive members of these orders, particularly the Flacourtiaceae and Sterculiaceae. A few others, including Hutchinson (1969) and Airy Shaw (1965, 1973) have proposed that the family is polyphyletic, with relatives among both the rosids and dilleniids.

In order to examine the systematic value of foliar morphology in general and to try to shed some light on the relationships of the Euphorbiaceae, I chose to work with the Phyllanthoideae, which is generally recognized to be the most primitive subfamily because many of its members have petaliferous flowers that, although unisexual, contain large androecial or gynoecial rudiments. This subfamily of 57 genera and about 2,000 species can be recognized by its lack of latex; alternate, stipulate leaves; tricolporate to porate, non-spinose pollen; biovulate locules; and ecarunculate seeds. In this paper I will describe phyllanthoid foliar morphology and discuss its bearing on the ancestry of the Euphorbiaceae. In later papers (Levin, 1986 and in press) I will present results of phenetic and cladistic analyses of the leaf characters that demonstrate that they do vary in taxonomically and phylogenetically meaningful ways.

MATERIALS AND METHODS

I examined leaves of 259 species belonging to 49 genera that Webster (1975) included in the Phyllanthoideae. I was unable to obtain leaves of *Apodiscus* Hutch., *Chascotheca* Urb., *Choriandrachne* Airy Shaw, *Danguyodrypetes* Leandr., *Gonatogyne* Muell. Arg., *Oreoporanthera* Hutch., *Pleiostemon* Sond., and *Securinega* sensu stricto. I also studied leaves from *Martretia* and *Paradrypetes,* genera that are usually included in the Phyllanthoideae but were excluded by Webster. For all but the very largest genera (e.g., *Glochidion* and *Phyllanthus*), my sample includes a minimum of 10% of the species.

Leaves were removed from herbarium specimens and cleared and stained according to the method of Wolfe (cited in Dilcher, 1974), except that some were mounted in Eukitt rather than Permount. Most were photographed with Kodak Technical Pan Film SO-115, a black-and-white, panchromatic negative film with extended red sensitivity, which was then developed and printed for maximum contrast. The resulting prints frequently showed details of venation more clearly than the original cleared leaves. Additional photomicrographs were taken with Kodak Panatomic-X, often using a green filter to enhance contrast. Cleared leaves and negatives are stored in the collections of Dr. Jack Wolfe, United States Geological Survey, Denver, Colorado, and the current author. Specimens and their vouchers are listed below with the descriptions of their respective genera. Because each species was rarely represented by more than a few cleared leaves from a single individual, I generally checked architectural characters on additional specimens of the same or closely related species. Whenever possible, herbarium specimens that had been annotated by authorities were chosen. In a few cases, I checked suspected determinations using the appropriate regional manuals or monographs.

Initially, each species was scored individually. I then grouped species into homogeneous groups. Most of these groups correspond to genera, subgenera, or sections, following Pax and Hoffmann (1922) for most genera, Jablonsky (1915) for *Bridelia* and *Cleistanthus,* and more recent monographs when these were available. In a few cases (e.g., *Bridelia, Drypetes*) the species within a sec-

tion formed two or more homogeneous groups, one or more of which was highly similar in architectural and epidermal characters to groups belonging to other sections. In these cases I disregarded the taxonomy and lumped similar species into a single group. Following the terminology of numerical taxonomists, I will refer to the homogeneous groups as operational taxonomic groups, or OTUs, in this and future papers (Levin, 1986 and in press). Table 1 lists the OTUs included in this study.

Characters

Leaf architectural terminology generally follows Hickey (1971, 1973). Leaf size classes are those of Raunkiaer (1934); nothing about venation is implied by the terms microphyll or megaphyll. Terminology for cuticular characters generally follows Dilcher (1974), who systematized Stace's (1965) terms. Specific trichome types follow Payne (1977) and stomatal terminology includes terms introduced by Payne (1970, 1979). I also recorded a few features of the leaf's internal anatomy, including type and distribution of crystals, degree and extent of sclerification of the bundle sheath, size of the terminal tracheids relative to the other tracheary elements in the freely-ending veinlets, and prominent idioblasts.

A few characters that I scored exhibited considerable variation within groups that were otherwise homogeneous. These characters include size and shape of the leaf, shape of the apex and base (with the exception of base balance), relative size of the terminal tracheids, sclerification of the bundle sheath, ultimate marginal venation, epidermal cell size, and trichome density. The last three of these have been shown in other groups to be sensitive to the environmental conditions under which the leaf developed (Stace, 1965; Sharma & Dunn, 1969; Lucic, 1970; Ehleringer & Bjorkman, 1978); such phenotypic plasticity would be particularly troublesome with small sample sizes such as mine. Marginal venation and sclerification of the bundle sheath can also show evolutionary instability, at least in the Magnoliaceae (Tucker, 1977) and *Hibbertia* (Rury & Dickison, 1977). Leaf shape characters are frequently used in keys to species in the Phyllanthoideae, suggesting that shape varies considerably at the species level, possibly in response to interspecific ecological differences, and thus will not be useful at higher taxonomic levels.

When I eliminated those characters that varied too much or that were monomorphic within the Phyllanthoideae, 43 characters remained. The character states for these characters and their codes are listed in Table 2. The order of character states within a character does not necessarily imply any evolutionary sequence. The following characters require more explanation:

3. Margin. In most members of the Aporuseae, the margins are entire to crenulate with small glands in the sinuses (Figs. 64–67). See the descriptions of this tribe for more details of this condition, which I recorded as state G. Three genera, *Bischofia, Drypetes,* and *Putranjiva,* bear theoid teeth. See the descriptions of these genera for a more thorough discussion of the tooth morphology.

4. Venation. I recognized two expressions of brochidodromous venation. In the first, state B, the secondary loop ends abruptly and, if it is accompanied by outer loops, these are formed by well differentiated secondary, tertiary, and quaternary veins (Figs. 32, 34). In the second, state W, the secondary loop is accompanied by additional secondary loops that gradually decrease in size and merge into tertiary loops (Figs. 31, 36, 97), a pattern I will refer to as weakly brochidodromous. This pattern differs from eucamptodromy (state U) in that in the latter the connections between one secondary and its superadjacent secondary are not formed by prominent secondary loops but are simply higher order crossveins (Figs. 41, 44). In the Phyllanthoideae, weak brochidodromy may form the evolutionary link between eucamptodromy and simple brochidodromy.

7. Angle of origin of basal secondary. If the angle formed between the lowermost pair of secondary veins and the midrib was consistent with the angles formed by the other lower secondaries (Figs. 14, 36, 97), I recorded state S; if the basal angle was either markedly more acute (Figs. 55, 64) or more obtuse (Figs. 3, 62), I recorded states A or O, respectively.

12. Size of outer loops. The sizes of the loops, if any, accompanying a secondary loop may be uniform (Fig. 90), decrease upward from the secondary loop (Fig. 55), or vary irregularly (Figs. 90, 119).

17. Composite intersecondary frequency. The three classes I recognized appear to have well marked boundaries in the Phyllanthoideae.

18. Intramarginal vein. In some sections of *Bridelia* the outer portions of the secondary loops form a vein at the leaf margin (Figs. 37, 38).

TABLE 1. Character states of taxa studied. Sequence of genera follows Webster (1975). Two genera that were examined, *Poranthera* and *Reverchonia*, are not included in the table because their extremely xeromorphic leaves provided few characters; they are described in full in the text. See Table 2 and text (pp. 30, 39) for explanation of character states. Numbers in parentheses refer to operational taxonomic units (OTUs) used in numerical analyses published elsewhere (Levin, 1986 and in press).

	Wielandia (1)	*Astrocasia* (2)	*Blotia* (9)	*Discocarpus* (5)	*Heywoodia* (3)	*Lachnostylis* (4)	*Pentabrachium* (13)	*Petalodiscus* (8)	*Savia* § *Heterosavia* (6)	*S.* § *Savia* (7)	*Amanoa* (10)	*Actephila* group 1 (11)	*Actephila* group 2 (12)	*Croizatia* (93)	*Bridelia* group 1 (14)	*Bridelia* group 2 (15)	*Bridelia* group 3 (16)	*Cleistanthus acuminatissimus* (17)	*C.* § *Stipulati* (18)	*C.* group 3 (19)	*C.* § *Chartacei* (20)	*C.* § *Cleistanthus* (21)	*C. saichikii* (22)	*C.* § *Australes* (23)	*C.* § *Leiopyxis* (24)	*Dicoelia* (25)	*Andrachne* group 1 (26)	*A.* § *Phyllanthopsis* (27)	*Spondianthus* (28)	*Antidesma* group 1 (29)	*A.* group 2 (30)	*A.* § *Tetrandra* (31)
1. Organization	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
2. Basal balance	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
3. Margin	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E
4. Venation	B	B	B	B	B	B	U	B	B	B	B	B	W	B	W	U	B	W	W	U	B	U	W	B	W	W	B	B	B	W	W	B
5. Primary size	m	m	m	m	m	S	m	m	m	m	m	S	m	m	S	S	S	S	S	S	S	S	m	S	m	m	S	m	m	m	m	S
6. 2° angle	M	M	W	M	M	M	M	M	M	M	M	W	M	W	M	M	M	M	M	N	W	N	M	W	M	M	N	N	M	M	M	M
7. Angle, basal 2°	S	O	S	S	A	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	O	A	S	A
8. Angle, lower 2°	S	S	A	S	S	S	A	A	S	S	S	S	S	A	O	O	O	O	S	S	S	S	S	S	S	A	O	S	S	S	S	S
9. Angle, upper 2°	S	O	S	S	O	S	S	S	S	S	S	S	S	S	S	A	A	O	O	O	S	O	O	S	O	S	S	S	S	S	S	S
10. 2° course	A	A	A	A	U	A	U	A	A	A	A	A	A	A	A	U	U	A	A	U	A	U	A	A	A	U	A	A	A	A	A	A
11. 2° loop angle	A	A	O	R	R	A	O	R	R	A	A	A	A	R	A	O	O	R	R	R	R	R	R	R	R	R	A	A	R	R	R	R
12. Outer loop size	U	U	U	U	U	U	D	U	U	U	D	D	D	U	D	A	A	D	D	D	U	D	D	U	D	D	D	I	D	D	D	U
13. 3° angle, admedial	A	R	R	A	R	A	R	R	A	A	O	R	R	A	R	R	R	A	R	R	R	O	R	R	R	R	R	R	R	R	R	R
14. 3° angle, exmedial	R	R	R	R	R	R	A	R	R	R	A	R	R	R	R	R	R	R	R	R	R	R	R	R	R	A	A	R	R	A	A	A
15. 3° pattern	R	W	O	W	R	R	W	O	O	O	R	R	p	W	p	p	p	p	p	W	W	W	W	O	W	p	W	W	R	W	W	O
16. Simple intersecond.	–	–	+	–	+	–	–	–	+	+	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
17. Composite intersecond.	F	A	I	I	A	A	A	F	A	I	I	F	I	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	I	A	A	A
18. Intramarginal vein	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
19. High order pattern	R	o	o	O	o	R	O	O	R	O	r	R	R	o	o	O	O	O	O	O	o	O	O	R	R	O	o	r	R	o	o	o
20. High order, size	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
21. Highest order present	5	6	6	5	5	6	6	5	5	5	6	5	5	5	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5

TABLE 1. Continued.

	Wielandia (1)	*Astrocasia* (2)	*Blotia* (9)	*Discocarpus* (5)	*Heywoodia* (3)	*Lachnostylis* (4)	*Pentabrachium* (13)	*Petalodiscus* (8)	*Savia* § *Heterosavia* (6)	*S.* § *Savia* (7)	*Amanoa* (10)	*Actephila* group 1 (11)	*Actephila* group 2 (12)	*Croizatia* (93)	*Bridelia* group 1 (14)	*Bridelia* group 2 (15)	*Bridelia* group 3 (16)	*Cleistanthus acuminatissimus* (17)	*C.* § *Stipulati* (18)	*C.* group 3 (19)	*C.* § *Chartacei* (20)	*C.* § *Cleistanthus* (21)	*C. saichikii* (22)	*C.* § *Australes* (23)	*C.* § *Leiopyxis* (24)	*Dicoelia* (25)	*Andrachne* group 1 (26)	*A.* § *Phyllanthopsis* (27)	*Spondianthus* (28)	*Antidesma* group 1 (29)	*A.* group 2 (30)	*A.* § *Tetrandra* (31)
22. Areole development	I	I	D	D	I	D	I	D	I	D	I	I	I	I	I	I	I	I	I	I	I	I	D	I	I	I	I	I	I	I	I	I
23. Areole arrangement	R	R	R	O	R	R	R	O	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
24. Areole shape	I	I	R	R	I	I	I	R	I	R	I	I	I	I	I	I	I	I	I	I	I	I	R	I	I	I	I	I	I	I	I	I
25. Areole size	M	M	M	S	M	M	M	M	M	M	M	M	M	M	M	M	S	M	M	M	L	M	M	M	S	M	M	S	M	M	M	M
26. Veinlets	2	2	S	A	3	2	2	S	2	S	3	2	2	2	2	2	S	2	2	2	2	2	2	2	2	2	S	S	2	2	2	2
27. Prismatic, mesophyll	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
28. Prismatic, veins	+	–	–	–	–	+	–	–	–	–	–	–	–	–	+	+	+	–	+	+	–	+	–	+	–	–	–	–	–	–	–	–
29. Druses, mesophyll	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
30. Druses, veins	–	+	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
31. Epidermal wall, adaxial	S	S	S	U	S	S	U	S	S	S	S	U	U	S	S	S	S	U	U	U	S	U	U	U	U	U	U	U	S	U	U	U
32. Epidermal wall, abaxial	S	S	S	U	S	S	U	S	S	S	S	U	U	S	S	S	S	U	U	U	S	U	U	U	U	U	U	U	S	U	U	U
33. Epidermal papillae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
34. Stomatal location	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	b	L	L	L	L	L	L	L	L	L	L
35. Stomatal index	B	B	C	C	B	C	B	C	C	C	B	B	B	B	B	B	B	B	B	B	A	B	B	B	B	B	B	B	B	B	B	B
36. Stomatal type	P	P	P	P	P	P	P	P	P	P	P	A	A	P	P	P	P	P	P	P	P	P	P	P	P	P	A	A	P	P	P	P
37. Water stomata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
38. Unicellular trichomes	A	A	A	A	A	A	S	A	A	A	A	A	S	S	A	A	A	S	S	S	S	A	A	A	A	S	S	S	A	S	S	S
39. Multicellular trichomes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
40. Peltate trichomes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41. Filiform sclereids	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	+	+	–	–	–	–	–	–
42. Tannin. epidermal cells	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+
43. Sclerified epidermal cells	–	–	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 1. Continued.

	A. § *Montana* (32)	*A.* § *Velutinosa* (33)	*A.* § *Ghaesembilla* (34)	*Celianella* (35)	*Hyeronima* (36)	*Leptonema* (37)	*Thecacoris* (38)	*Aporusa* (39)	*Ashtonia* (40)	*Baccaurea* group 1 (41)	*B.* § *Pierardia* (42)	*B. Dubiae* (43)	*B.* § *Isoandrion* (44)	*Didymocistus* (45)	*Maesobotrya* (46)	*Protomegabaria* (47)	*Richeria* (48)	*Drypetes* group 1 (49)	*D.* group 2 (50)	*D.* group 3 (51)	*D.* group 4 (52)	*D.* group 5 (53)	*D.* group 6 (54)	*Neowawraea* (90)	*Putranjiva* (55)	*Jablonskia* (56)	*Keayodendron* (57)	*Lingelsheimia* (94)	*Meineckia* (58)	*Pseudolachnostylis* (59)	*Zimmermannia* (60)
1. Organization	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
2. Basal balance	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	A	A	A	A	A	A	S	A	S	S	S	S	S	S
3. Margin	E	E	E	E	E	E	E	G	G	G	G	G	G	E	G	E	G	T	T	E	T	T	T	E	T	E	E	E	E	E	E
4. Venation	B	W	W	B	W	B	B	B	B	W	W	B	B	W	W	W	W	B	W	U	B	B	B	W	B	B	B	B	B	B	B
5. Primary size	m	m	S	M	S	m	S	S	S	S	S	S	S	m	S	S	m	m	m	m	m	m	m	m	m	m	m	m	m	m	m
6. 2° angle	M	M	M	N	M	N	M	M	M	M	M	N	W	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	N	M	M
7. Angle, basal 2°	A	A	O	S	S	O	S	A	A	O	A	S	A	S	A	S	S	A	A	A	A	A	A	S	A	S	S	S	S	S	S
8. Angle, lower 2°	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	A	S	S	S	O	S
9. Angle, upper 2°	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	O	S	S	S	S	S	S	S	S	S	O	S	S	S	S	O
10. 2° course	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	U	A	A	A	A	A	A	A	A	A	A	A
11. 2° loop angle	R	R	R	R	A	R	R	A	A	R	A	O	R	R	A	A	R	R	R	R	R	R	R	A	A	R	R	A	R	A	A
12. Outer loop size	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	U	D	A	U	U	U	D	U	U	U	D	D	D	D
13. 3° angle, admedial	R	R	R	R	R	R	R	R	R	R	O	R	R	R	R	O	R	R	R	R	R	R	R	R	O	R	R	R	R	R	R
14. 3° angle, exmedial	A	A	A	R	A	A	A	A	A	A	A	R	A	A	A	A	A	R	R	R	R	R	R	A	A	R	R	A	A	R	A
15. 3° pattern	O	W	W	W	W	W	O	W	W	p	P	W	W	p	p	p	W	O	O	W	O	r	O	p	O	O	O	W	W	W	W
16. Simple intersecond.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
17. Composite intersecond.	A	A	A	I	A	A	A	I	I	A	A	A	A	A	A	A	I	I	I	I	I	A	I	I	I	A	F	A	A	A	A
18. Intramarginal vein	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
19. High order pattern	o	o	o	R	o	o	o	o	o	o	r	o	o	O	o	o	o	o	o	O	o	r	O	O	o	o	R	o	R	O	o
20. High order, size	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	m	M	M
21. Highest order present	5	5	5	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6	5	4	5	6	5	5	5	5	4	5	5

TABLE 1. Continued.

	A. § *Montana* (32)	*A.* § *Velutinosa* (33)	*A.* § *Ghaesembilla* (34)	*Celianella* (35)	*Hyeronima* (36)	*Leptonema* (37)	*Thecacoris* (38)	*Aporusa* (39)	*Ashtonia* (40)	*Baccaurea* group 1 (41)	*B.* § *Pierardia* (42)	*B. Dubiae* (43)	*B.* § *Isoandrion* (44)	*Didymocistus* (45)	*Maesobotrya* (46)	*Protomegabaria* (47)	*Richeria* (48)	*Drypetes* group 1 (49)	*D.* group 2 (50)	*D.* group 3 (51)	*D.* group 4 (52)	*D.* group 5 (53)	*D.* group 6 (54)	*Neowawraea* (90)	*Putranjiva* (55)	*Jablonskia* (56)	*Keayodendron* (57)	*Lingelsheimia* (94)	*Meineckia* (58)	*Pseudolachnostylis* (59)	*Zimmermannia* (60)
22. Areole development	I	I	D	I	I	I	I	I	I	I	i	I	i	D	i	I	I	I	I	D	I	i	D	D	I	I	I	I	I	D	I
23. Areole arrangement	R	R	R	R	R	R	R	R	R	R	R	R	R	O	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	O	R
24. Areole shape	I	I	I	I	I	I	I	I	I	I	I	I	I	R	I	I	I	I	I	I	R	I	R	R	I	I	I	I	I	R	I
25. Areole size	M	M	S	M	M	M	M	M	M	M	L	M	M	S	M	M	M	M	M	M	L	L	S	S	M	M	M	M	M	S	M
26. Veinlets	2	2	2	2	2	2	2	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	S	2	2	2	2	2	2	S	2
27. Prismatic, mesophyll	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	–	–	–	–	–	–	–	–	–	–
28. Prismatic, veins	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+	+	–	–	–	–	–	–	–
29. Druses, mesophyll	–	–	–	–	–	–	–	+	–	+	+	+	+	–	+	–	+	+	–	–	–	–	–	–	–	–	+	+	–	–	–
30. Druses, veins	–	–	–	–	–	–	–	+	–	+	+	+	+	–	+	+	+	–	–	–	–	–	–	–	–	–	+	+	–	+	–
31. Epidermal wall, adaxial	U	U	U	S	S	S	U	S	S	S	U	U	S	S	S	S	S	U	U	U	U	U	U	S	S	S	S	S	U	S	S
32. Epidermal wall, abaxial	U	U	U	S	S	S	U	S	S	S	U	U	U	S	U	S	S	U	U	U	U	U	U	S	S	S	S	S	U	S	S
33. Epidermal papillae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–
34. Stomatal location	L	L	b	L	L	B	L	L	L	L	L	L	L	L	L	b	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
35. Stomatal index	B	B	C	C	B	C	B	B	B	B	B	B	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
36. Stomatal type	P	P	P	P	P	P	P	A	A	A	A	A	A	P	A	A	A	P	P	P	P	P	P	P	P	P	P	P	P	P	P
37. Water stomata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
38. Unicellular trichomes	S	S	S	A	A	S	S	S	S	T	A	S	S	T	S	S	S	A	A	A	A	A	A	A	A	A	S	A	A	S	A
39. Multicellular trichomes	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
40. Peltate trichomes	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41. Filiform sclereids	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
42. Tannin. epidermal cells	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
43. Sclerified epidermal cells	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 1. Continued.

	Flueggea (16)	*Breynia* (62)	*Glochidion* § *Glochidion* (63)	*G.* group 2 (64)	*G.* group 3 (65)	*Margaritaria* (67)	*Phyllanthus* § *Adenoglochidion* (68)	*P.* § *Anisonema* (69)	*P.* § *Aporosella* (70)	*P.* § *Cicca* (71)	*P.* § *Eleutherogynium* (72)	*P.* § *Emblica* (73)	*P.* § *Floribundi* (74)	*P.* subg. *Gomphidium*, group 1 (75)	*P.* subg. *Gomphidium*, group 2 (76)	*P.* § *Hemicicca* (77)	*P.* § *Heteroglochidion* (78)	*P.* § *Nothoclema* (79)	*P.* § *Nymphanthus* (80)	*P.* § *Paragomphidium* (81)	*P.* § *Phyllanthodendron* (82)	*P.* § *Polyandroglochidion* (83)	*P.* § *Psychoglochidion* (84)	*P.* § *Scepasma* (85)	*Richeriella* (86)	*Sauropus* (87)	*Synostemon* (66)	*Uapaca* (88)	*Hymenocardia* (89)	*Bischofia* (91)	*Martretia* (92)
1. Organization	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	C	S
2. Basal balance	S	S	S	S	A	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	A	S	S	A	S	S	S	S	S	S
3. Margin	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	T	E
4. Venation	W	W	W	W	W	B	B	W	W	W	B	W	B	B	B	W	B	W	W	B	W	B	B	B	B	W	W	U	W	B	B
5. Primary size	m	m	S	S	S	m	m	m	m	m	m	S	S	S	S	m	m	m	m	S	m	m	m	m	m	m	m	S	S	m	S
6. 2° angle	M	M	M	M	M	M	M	M	M	M	N	N	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M
7. Angle, basal 2°	S	S	S	S	S	S	S	S	S	O	O	O	S	O	S	S	S	S	O	O	S	S	S	S	S	S	S	S	A	S	S
8. Angle, lower 2°	S	O	O	A	S	S	S	S	S	S	S	S	S	S	O	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	A
9. Angle, upper 2°	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	O	S	S	S	S	S	S	S	S	O	S	S	S	A	S
10. 2° course	A	A	A	A	A	A	A	A	A	A	A	U	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
11. 2° loop angle	A	A	A	A	A	A	A	A	A	A	O	R	A	A	A	O	A	A	A	A	O	A	O	R	R	A	A	R	A	O
12. Outer loop size	D	D	D	D	D	U	U	D	D	D	U	D	U	U	I	D	U	D	D	U	D	I	U	I	U	D	D	A	D	U	I
13. 3° angle, admedial	R	O	R	R	R	R	R	R	R	R	R	A	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	O
14. 3° angle, exmedial	R	A	R	R	A	R	A	A	A	A	R	A	A	A	R	A	R	A	A	A	A	R	A	R	A	A	R	A	R	A	R
15. 3° pattern	p	p	P	p	P	W	O	W	W	W	R	R	W	W	R	W	W	W	O	R	p	r	W	R	W	p	R	p	W	R	O
16. Simple intersecond.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
17. Composite intersecond.	A	A	A	A	A	I	A	F	F	F	A	F	I	I	A	I	I	I	F	A	I	A	F	A	F	I	A	I	A	A	F
18. Intramarginal vein	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
19. High order pattern	o	o	o	o	o	o	o	o	o	o	R	R	R	o	R	R	R	o	R	R	o	r	o	o	o	o	R	o	O	R	R
20. High order, size	M	M	M	M	M	M	M	M	M	M	h	M	M	M	h	M	M	M	M	h	M	M	M	M	M	M	F	M	M	M	M
21. Highest order present	5	5	5	5	5	5	6	5	6	5	5	5	5	5	4	5	5	5	5	5	5	4	5	4	5	6	4	5	6	5	5

TABLE 1. Continued.

	Flueggea (16)	*Breynia* (62)	*Glochidion* § *Glochidion* (63)	*G.* group 2 (64)	*G.* group 3 (65)	*Margaritaria* (67)	*Phyllanthus* § *Adenoglochidion* (68)	*P.* § *Anisonema* (69)	*P.* § *Aporosella* (70)	*P.* § *Cicca* (71)	*P.* § *Eleutherogynium* (72)	*P.* § *Emblica* (73)	*P.* § *Floribundi* (74)	*P.* subg. *Gomphidium*, group 1 (75)	*P.* subg. *Gomphidium*, group 2 (76)	*P.* § *Hemicicca* (77)	*P.* § *Heteroglochidion* (78)	*P.* § *Nothoclema* (79)	*P.* § *Nymphanthus* (80)	*P.* § *Paragomphidium* (81)	*P.* § *Phyllanthodendron* (82)	*P.* § *Polyandroglochidion* (83)	*P.* § *Psychoglochidion* (84)	*P.* § *Scepasma* (85)	*Richeriella* (86)	*Sauropus* (87)	*Synostemon* (66)	*Uapaca* (88)	*Hymenocardia* (89)	*Bischofia* (91)	*Martretia* (92)
22. Areole development	I	I	I	I	I	I	I	I	I	I	I	I	I	I	i	I	I	I	I	I	I	i	I	I	I	I	I	D	i	I
23. Areole arrangement	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
24. Areole shape	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	R	I	I
25. Areole size	S	M	M	M	M	S	M	S	S	S	M	S	S	M	M	M	M	S	M	M	M	M	M	S	M	S	S	S	M	M
26. Veinlets	2	2	2	2	2	2	2	2	2	2	2	S	2	2	2	S	2	2	2	2	2	2	3	2	2	2	S	2	2	2
27. Prismatic, mesophyll	–	–	–	–	–	–	–	+	–	–	+	–	+	–	+	–	+	+	–	–	–	–	+	–	–	–	–	–	–	–
28. Prismatic, veins	–	–	–	–	–	–	–	+	+	–	+	–	+	–	+	–	+	+	–	–	–	+	+	–	–	–	–	–	+	–
29. Druses, mesophyll	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–
30. Druses, veins	+	+	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	+
31. Epidermal wall, adaxial	S	U	S	S	S	S	S	S	S	S	S	S	S	S	U	U	S	S	S	S	U	S	S	S	S	U	S	S	S	U
32. Epidermal wall, abaxial	S	U	U	U	U	S	S	S	S	S	S	S	S	S	U	U	S	S	S	S	S	S	U	S	S	U	U	S	S	U
33. Epidermal papillae	+	+	–	–	+	+	–	–	–	–	–	–	–	+	+	–	–	–	–	+	–	–	–	–	–	–	+	–	–	–
34. Stomatal location	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	B	L	L	L	b
35. Stomatal index	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
36. Stomatal type	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	A	P	P	P
37. Water stomata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
38. Unicellular trichomes	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	S	S	A	A
39. Multicellular trichomes	–	+	+	+	+	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–
40. Peltate trichomes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
41. Filiform sclereids	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
42. Tannin. epidermal cells	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
43. Sclerified epidermal cells	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 2. Characters and character states. See Hickey (1973), Dilcher (1974), and text (pp. 30, 39) for more explanation.

1. Organization: Simple = S; Compound = C.
2. Base balance: Symmetrical = S; Asymmetrical = A.
3. Margin: Entire = E; Entire or crenate, but with glands = G; Toothed = T.
4. Venation: Brochidodromous = B; Weakly brochidodromous = W; Eucamptodromous = U.
5. Primary size: Moderate = m; Stout = S; Massive = M.
6. Secondary angle: Narrow (<45°) = N; Moderate = M; Wide (>65°) = W.
7. Angle of basal secondaries, relative to adjacent secondaries: More acute = A; Similar = S; More obtuse = O.
8. Angle of lower secondaries, relative to middle secondaries: More acute = A; Similar = S; More obtuse = O.
9. Angle of upper secondaries, relative to middle secondaries: More acute = A; Similar = S; More obtuse = O.
10. Secondary course: Curved uniformly = U; Curved abruptly = A.
11. Angle of secondary loops: Acute = A; Right = R; Obtuse = O.
12. Size of outer loops: Irregular = I; Uniform = U; Decreasing upwards = D; Absent = A.
13. Tertiary angle of origin, admedial: Acute = A; Right = R; Obtuse = O.
14. Tertiary angle of origin, exmedial: Acute = A; Right = R; Obtuse = O.
15. Tertiary pattern: Ramified = r; Random reticulate = R; Orthogonal reticulate = O; Weakly percurrent = W; Strongly percurrent, angle to midrib oblique = p; Strongly percurrent, angle to midrib predominantly right = P.
16. Simple intersecondaries: Absent = −; Present = +.
17. Composite intersecondaries: Absent = A; Infrequent (in fewer than 20% of intercostal areas) = I; Frequent (in more than 20% of intercostal areas) = F.
18. Intramarginal vein: Absent = −; Present = +.
19. Higher order vein pattern: Ramified = r; All random = R; 4° orthogonal, higher orders random = o; 4° and 5° orthogonal = O.
20. Higher order vein size: All moderate = M; 4° moderate, 5° fine = m; 4° and 5° fine = F; 4° moderate, 5° heavy = h.
21. Highest order present: 4° = 4; 5° = 5; 6° = 6.
22. Areole development: Incomplete = i; Imperfect = I; Well-developed = D.
23. Areole arrangement: Random = R; Ordered = O.
24. Areole shape: Irregular = I; Regular = R.
25. Areole size: Large = L; Medium = M; Small = S.

TABLE 2. Continued.

26. Veinlets: Absent = A; Simple = S; Branched 1–2× = 2; Branched 2–3× = 3.
27. Prismatic crystals in mesophyll: Absent = −; Present = +.
28. Prismatic crystals with veins: Absent = −; Present = +.
29. Druses in mesophyll: Absent = −; Present = +.
30. Druses with veins: Absent = −; Present = +.
31. Epidermal anticlinal walls, adaxial: Straight = S; Undulate = U.
32. Epidermal anticlinal walls, abaxial: Straight = S; Undulate = U.
33. Epidermal papillae: Absent = −; Present = +.
34. Stomatal location: Abaxial only = L; Primarily abaxial, but a few adaxial = b; Approximately equal on both surfaces = B.
35. Stomatal index (abaxial): <10% = A; 10–20% = B; >20% = C.
36. Stomatal type: Paracytic = P; Anisocytic = A.
37. Water stomata: Absent = −; Present = +.
38. Unicellular trichomes: Absent = A; Solitary = S; Some tufted = T.
39. Uniseriate, multicellular trichomes: Absent = −; Present = +.
40. Peltate trichomes: Absent = −; Present = +.
41. Filiform sclereids in mesophyll: Absent = −; Present = +.
42. Tanniferous epidermal cells: Absent = −; Present = +.
43. Sclerified epidermal cells: Absent = −; Present = +.

Although technically marginal in position because no leaf tissue lies outside of it, this vein appears to be homologous to Hickey's (1973) intramarginal vein and I will use his term. See the description of *Bridelia* for more details.

26. Veinlets. The degree of branching of the freely-ending veinlets did not break down cleanly into simple, branched once, branched twice, etc. Instead, several degrees of branching were usually present within even a single leaf, although most veinlets branched within a limited range of degrees. The classes absent, simple (unbranched), branched 1–2 times, and branched 2–3 times appeared to reflect the variation more accurately.

35. Stomatal index. These classes appear to represent natural ranges that are distinct from each other in the Phyllanthoideae.

36. Stomatal type. Because both paracytic and brachyparacytic (Dilcher, 1974) stomata occur in many taxa, or even on the same leaf in

many species in the Flueggeinae, I did not differentiate between these basically paracytic patterns in Tables 1 and 2. For the specific stomatal types, see the descriptions of the taxa.

37. Water stomata. Some *Andrachne* species bear large, apparently anomocytic stomata in addition to their more numerous, smaller anisocytic stomata (Fig. 54).

38. Unicellular trichomes. In the Phyllanthoideae, unicellular trichomes are usually simple with a peg-like, unmodified base and radial basal cells (Figs. 48, 57).

42. Tanniniferous epidermal cells. In several tribes, some of the epidermal cells are enlarged and spherical, with the adjacent cells forming a radial pattern (Figs. 58, 110). These contain tannins, according to Rothdauscher (1896) and Gaucher (1902); I have not attempted to confirm their reports.

43. Sclerified cells in the lower epidermis. See the descriptions of *Amanoa* and *Discocarpus* for more on these cells.

In addition to these characters, one character not among those listed in Table 2 but included in the descriptions below requires further explanation. Hickey (1971, 1977), based on his examination of cleared and fossil dicotyledon leaves, categorized the degree to which venation is organized into four levels or ranks. Rank is based primarily on the highest vein order in which the veins follow relatively regular courses and delimit areas of relatively consistent size and shape. If the secondary and higher order veins have irregular courses and the intercostal areas, therefore, are not uniform in size and shape, the organization is said to be first rank: only the primary vein has a regular course. If the secondary veins follow regular courses and the intercostal areas have uniform size and shape, but the tertiary and higher vein orders are disorganized, the level of organization is second rank. As the degree of organization increases further, the ranks increase to third and finally fourth, in which even the areoles show at least rudimentary orientation within domains. Leaves with low organizational rank appear first in the fossil record and, among living dicotyledons, the rank of foliar venation organization correlates well with the degree of advancement of the whole plant as determined by other evidence (Hickey, 1971, 1977; Hickey & Doyle, 1972; Doyle & Hickey, 1976).

In general, rank is fairly easy to assign by following Hickey's criteria. Problems may arise, however, with leaves from arid, arctic, or alpine habitats. In plants from these habitats, the organization of leaf venation frequently shows a regression below the level typical of their more temperate relatives, particularly in the lower vein orders (Hickey, 1977; Rury & Dickison, 1977). As a result, leaves can be found in which the higher order veins are more organized than are the lower order veins. It is not clear what ranks Hickey would assign in such cases. I recommend basing rank on the highest vein order that is regular in course, regardless of the behavior of lower order veins. In this way, the degree of evolutionary advancement achieved by the leaves will be better reflected by the rank assigned.

Results

Table 1 summarizes the distribution of character states for the characters in Table 2. Two genera that I examined, *Poranthera* and *Reverchonia,* are not included in Table 1 because the extremely xeromorphic leaves of these genera contain too few characters.

In the discussion that follows I will first describe the leaf architecture and cuticular features of the subfamily. I will then describe each genus in turn, following the sequence in Webster's (1975) classification, including only those characters that are not adequately summarized in Tables 1 and 2. At the end of the generic descriptions for each tribe, I will discuss the taxonomic implications of the foliar morphology.

Descriptions and Discussion

PHYLLANTHOIDEAE ASCHERSON

Leaves simple (compound in *Bischofia*), microphylls to mesophylls, some nanophylls; blades typically symmetrical, shape various; apex and base various; margin entire or crenate, toothed only in *Bischofia, Drypetes,* and *Putranjiva,* which bear theoid teeth; glands typically absent, if present then laminar or marginal; organization of venation typically second to third rank, but first or fourth rank in some; venation pinnate, brochidodromous to eucamptodromous, a few species kladodromous or reticulodromous; primary vein moderate to stout, rarely weak or massive, typically straight; secondary vein angle of divergence acute, uniform or varying, thickness moderate, curved uniformly or abruptly, loop-forming branches, if any, joining superadjacent secondary at acute to obtuse angle, only in *Bridelia* forming an intramarginal vein; intersecon-

dary veins simple, composite, or absent; tertiary veins originating at various angles, reticulate or percurrent, in a few species ramified admedially, if percurrent straight or sinuous, branched or unbranched, oblique to primary vein with angle constant or decreasing upward or outward, typically alternate; higher order venation random to orthogonal, typically resolved to fifth or sixth order; marginal ultimate venation various; areoles imperfect to well developed, incomplete in some, arrangement random or oriented, shape typically irregular, size small to large; veinlets simple to branched three times, rarely absent; terminal tracheids normal or swollen; bundle sheath of primary vein almost always sclerified, higher order veins parenchymatous or sclerified; epidermal cells isodiametric, arrangement random or tetragonal to polygonal, anticlinal cell walls straight or undulate and typically unornamented, surface smooth or papillate; stomata typically only abaxial, on both surfaces in a few, orientation random, stomatal index about 8–25%, paracytic, brachyparacytic, parallelocytic, anisocytic, or, rarely, anomocytic, development mesogenous or mesoperigynous; trichomes typically unicellular with peg-like base and radial basal cells, some uniseriate with an unmodified base, rarely multiseriate or with a multicellular or enlarged head or branched; domatia absent except in *Bischofia* with marsupiform domatia; crystals typically present within leaf, single and prismatic or druses.

WIELANDIEAE BAILL. EX HURUSAWA

Wielandia Baill. (OTU 1)

W. elegans Baill., Seychelles: *Bernardi 14639* (BM). Figures 1, 2.

Leaves large microphylls, symmetrical, ovate-elliptic; apex acute; base acute; organization of venation high second rank; ultimate marginal venation incomplete, veins thickened and heavily sclerified, flaring toward the margin (Fig. 2); terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic.

Astrocasia Robn. & Millsp. (OTU 2)

A. neurocarpa (Muell. Arg.) I. M. Johnst., Mexico: Tamaulipas, *Stanford et al. 2264* (SUDH). Figures 3, 4, 7.

A. peltata Standl., Mexico: Tres Marias Island, *Howell 10405* (CAS).

A. phyllanthoides Robn. & Millsp., Mexico: Yucatan, *Gaumer 475* (UC).

Leaves microphylls to small mesophylls, symmetrical, very wide ovate to orbiculate; apex rounded or emarginate; base rounded or peltate; organization of venation mid third rank; marginal ultimate venation fimbriate; terminal tracheids normal (*A. peltata, A. phyllanthoides*) or swollen (*A. neurocarpa*); bundle sheath parenchymatous (*A. phyllanthoides*) or sclerified (*A. neurocarpa, A. peltata*); stomata brachyparacytic; lower epidermis papillate (*A. phyllanthoides*) or smooth.

Blotia Leandri (OTU 9)

B. oblongifolia (Baill.) Leandri, Madagascar: *Serv. For. 6157* (P). Figures 5, 6.

Leaves mesophylls, symmetrical, narrow elliptic; apex acuminate; base obtuse; organization of venation low third rank; marginal ultimate venation fimbriate; terminal tracheids normal; bundle sheath of higher order veins lightly sclerified; stomata paracytic.

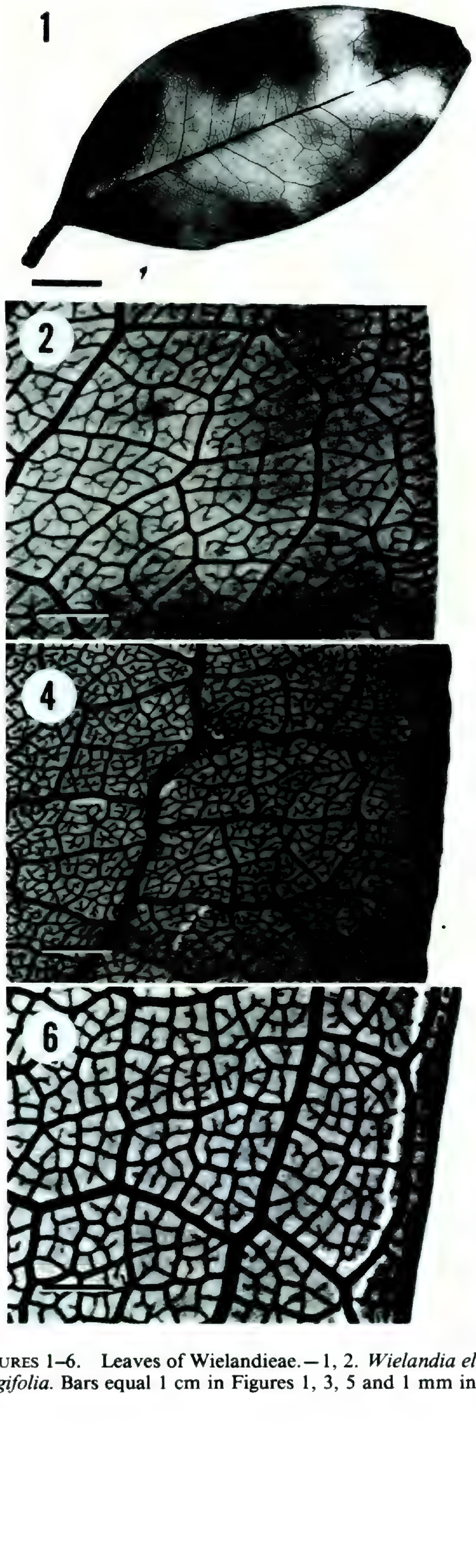
Discocarpus Klotzsch (OTU 5)

D. spruceanus Benth., Guiana: *Spruce 3527* (MO). Figures 8, 9.

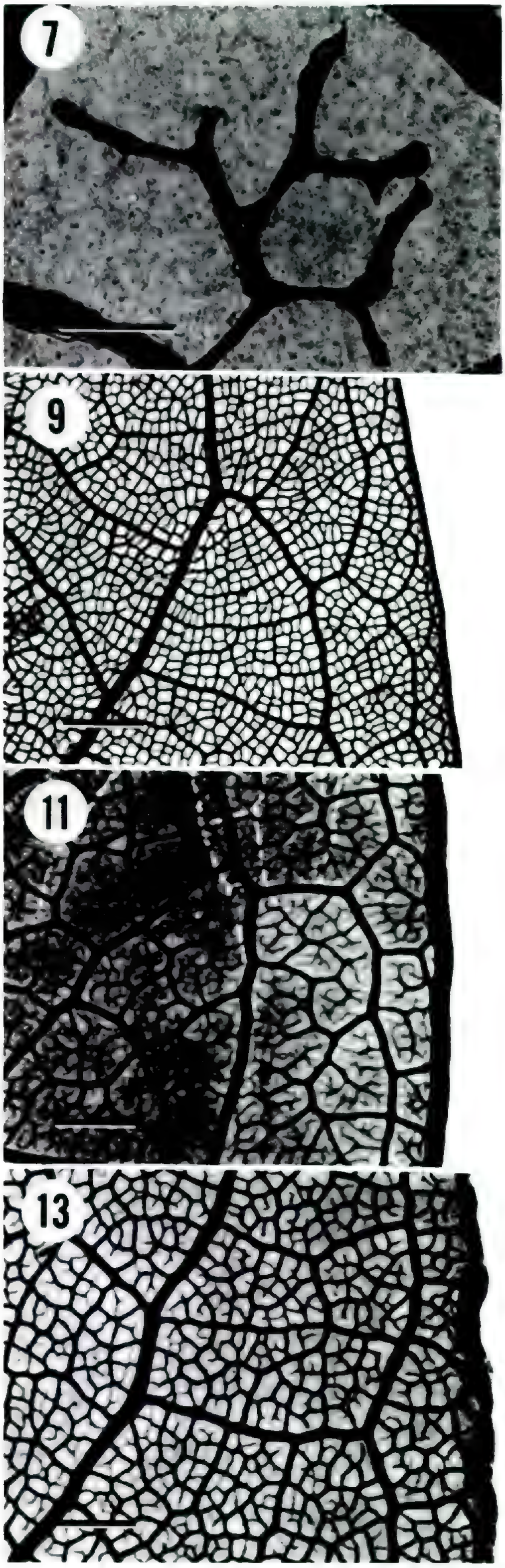
Leaves microphylls, symmetrical, elliptic; apex attenuate; base obtuse; organization of venation mid fourth rank (but see below); marginal ultimate venation fimbriate; terminal tracheids normal; bundle sheath of higher order veins parenchymatous, but extensions sclerenchymatous; stomata brachyparacytic.

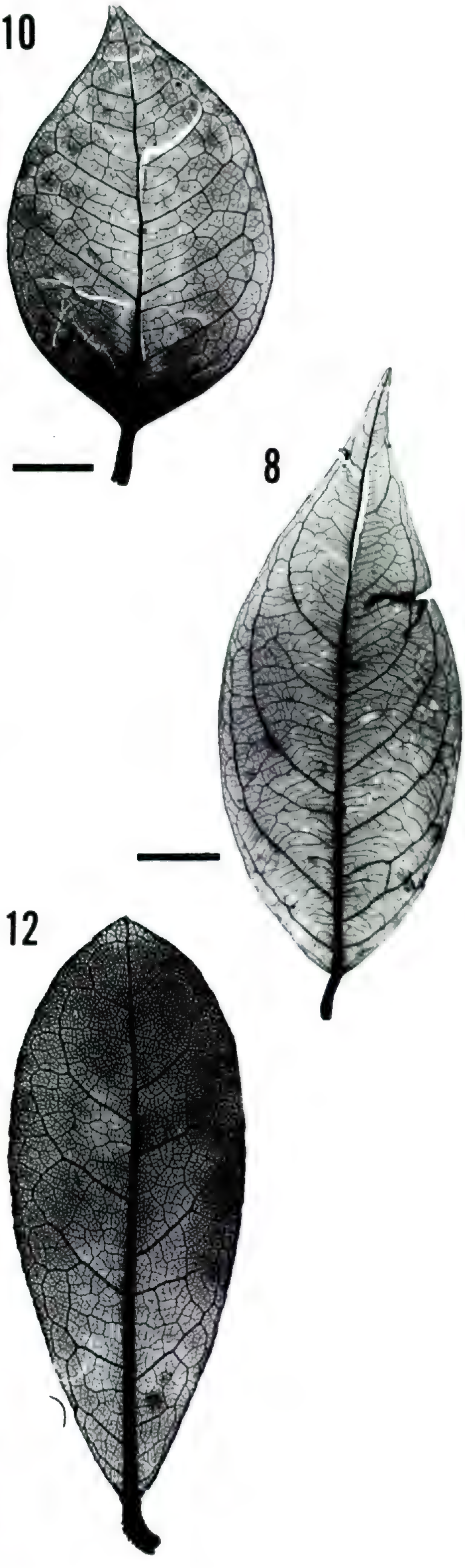
My anatomical observations agree with descriptions by Rothdauscher (1896) and Gaucher (1902).

The leaves of *Discocarpus* are remarkable in many respects. Although the higher order venation is strikingly orthogonal, forming extremely well developed areoles, the lower order venation is much less organized, with uncommon simple intersecondaries and weakly percurrent tertiaries that are quite irregular and sinuous in course. Freely-ending veinlets are rare, and when present are simple and straight. This pattern appears to be the result of a trend, involving several genera, of decreasing organization of lower order venation and increasing organization of higher order venation. Stomatal frequency is very high, with most cells in the lower epidermis appearing to be subsidiary cells



FIGURES 1–6. Leaves of Wielandieae.—1, 2. *Wielandia elegans.*—3, 4. *Astrocasia neurocarpa.*—5, 6. *Blotia oblongifolia.* Bars equal 1 cm in Figures 1, 3, 5 and 1 mm in Figures 2, 4, 6.





FIGURES 7–13. Leaves of Wielandieae.—7. *Astrocasia neurocarpa,* swollen terminal tracheids.—8, 9. *Discocarpus spruceanus.*—10, 11. *Heywoodia lucens.*—12, 13. *Lachnostylis hirta.* Bars equal 1 cm in Figures 8, 10, 12; 1 mm in Figures 9, 11, 13; and 100 μm in Figure 7.

or guard cells. The lower epidermis is also strongly sclerified, with the outer wall of most cells thickened (cf. *Amanoa,* below).

Heywoodia Sim. (OTU 3)
H. lucens Sim., Tanganyika: *Watkins 453* (EAH). Figures 10, 11.

Leaves microphylls, symmetrical, elliptic; apex acuminate; base obtuse-cuneate; tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic.

Lachnostylis Turcz. (OTU 4)
L. hirta (L. f.) Muell. Arg., South Africa: *Burchell 5213* (G). Figures 12, 13.

Leaves microphylls, symmetrical, oblanceolate; apex obtuse; base acute; organization of venation high second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins lightly sclerified; stomata brachyparacytic, rarely each subsidiary cell divided again by a wall perpendicular to the guard cells.

My anatomical observations agree with the reports of Rothdauscher (1896) and Gaucher (1902).

Pentabrachium Muell. Arg. (OTU 13)
P. reticulatum Muell. Arg., Cameroons: *Zenker 3869* (MO). Figures 14, 15.

Leaves mesophylls, symmetrical, ovate-elliptic; apex long acuminate; base obtuse; organization of venation mid third rank; marginal ultimate venation fimbriate; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes scattered on abaxial epidermis.

Petalodiscus Baill. (OTU 8)
P. danguyana Leandri, Madagascar: *Schlieben 8120* (UC). Figures 16, 17.

Leaves microphylls, symmetrical, narrow ovate-elliptic; apex acuminate; base obtuse; organization of venation low fourth rank (but see below); marginal ultimate venation incomplete to weakly looped; terminal tracheids normal; bundle sheath of higher order veins lightly sclerified; stomata paracytic.

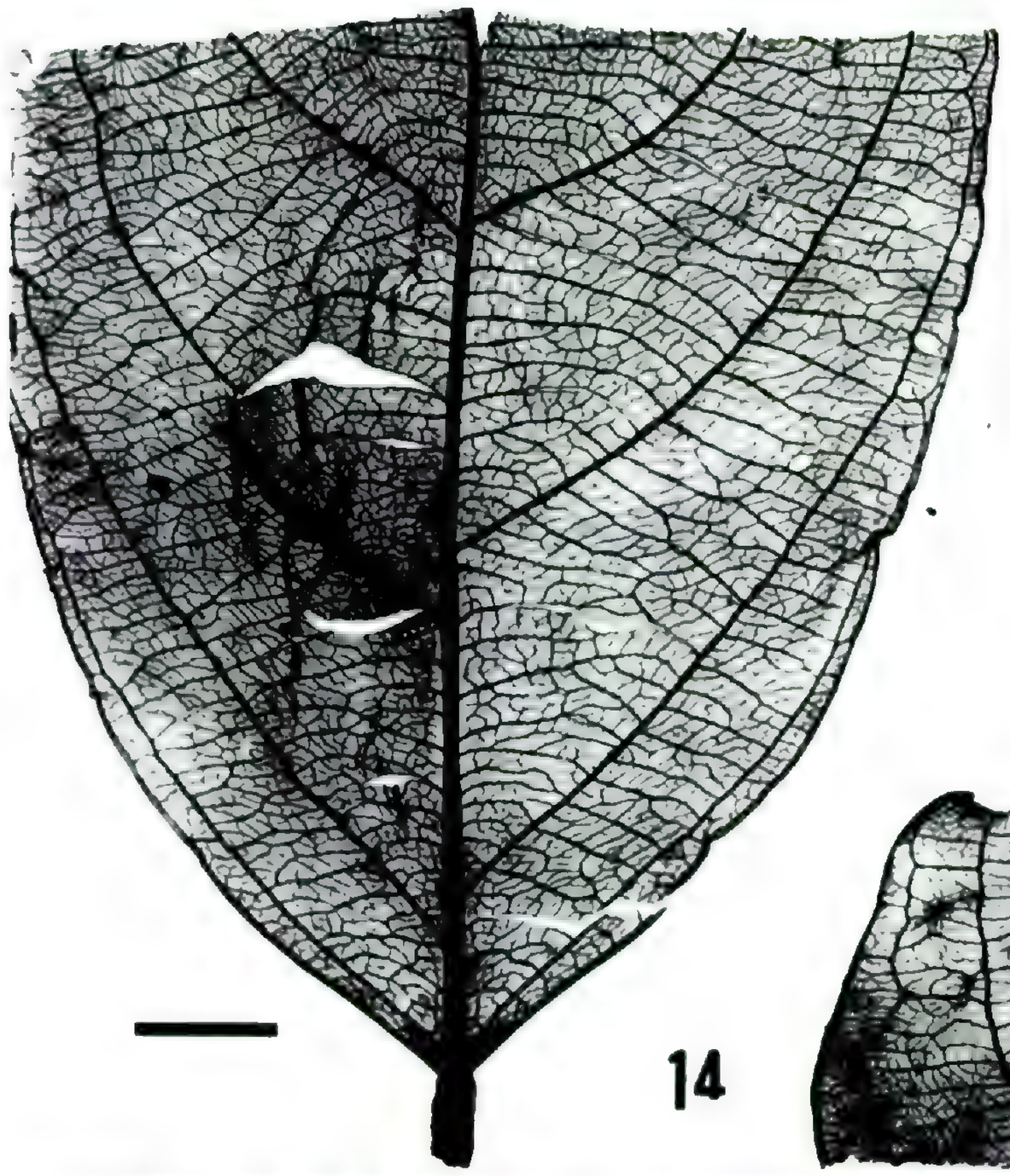
The leaves of *Petalodiscus,* as do those of *Discocarpus,* exhibit an unusual combination of relatively disorganized lower order venation with highly differentiated orthogonal higher order venation forming oriented, but still imperfect areoles.

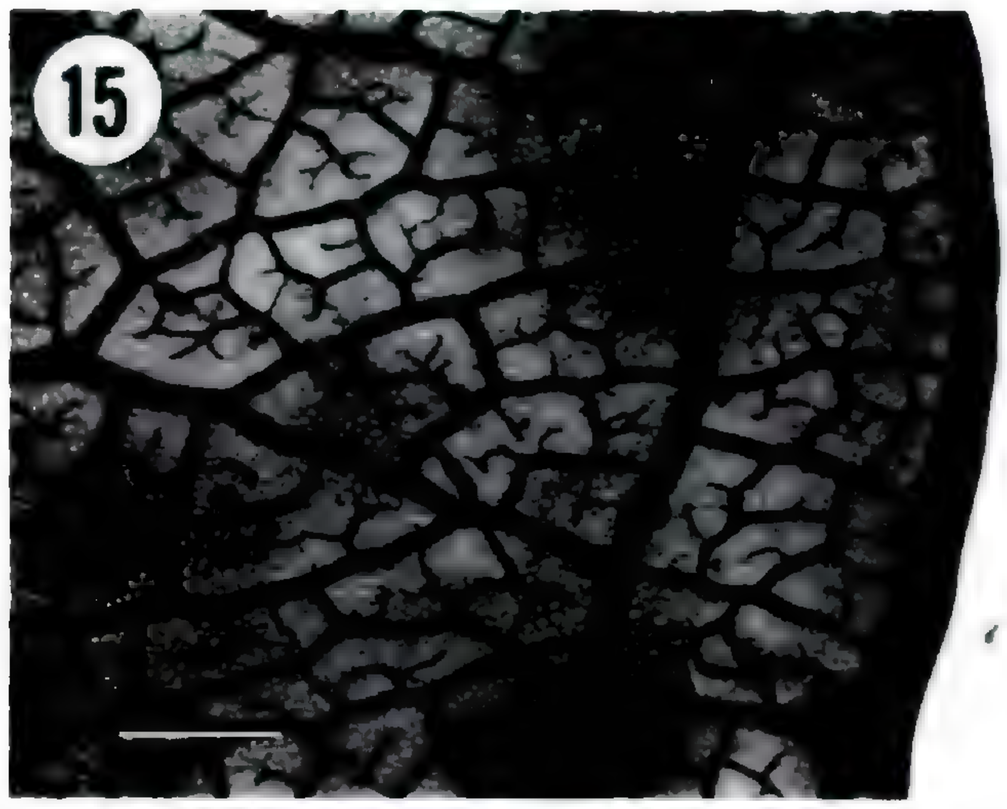
Savia Willd.
Sect. *Heterosavia* Urb. (OTU 6)
S. bahamensis Britt., U.S.A.: Florida, *Caldwell 8782* (UC). Figures 18, 19, 22.
S. clementis Alain, Cuba: *Clemente et al. 4036* (DAV).
S. clusiifolia Griseb., Cuba: *Alain & Clemente 1485* (DAV).
S. cuneifolia Urb., Cuba: *Alain & Clemente 919* (DAV).
S. erythroxyloides Griseb., Haiti: *Leonard 8334* (UC).
Sect. *Savia* (OTU 7)
S. sessiliflora Willd., Haiti: *Holdridge 1415* (UC). Figures 20, 21.

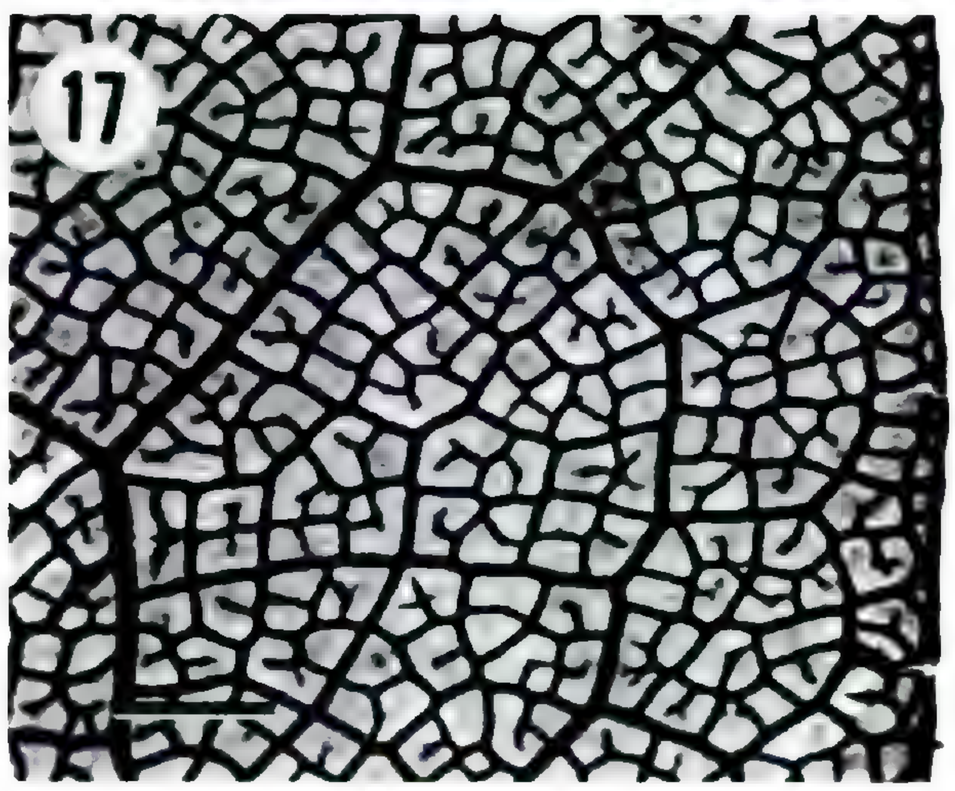
Leaves microphylls, symmetrical, obovate or elliptic; apex acute, obtuse, rounded, or emarginate; base acute-decurrent or cuneate or obtuse; organization of venation low to mid third rank; marginal ultimate venation looped or fimbriate; terminal tracheids normal; bundle sheath of higher order veins parenchymatous or lightly sclerified; stomata paracytic or occasionally parallelocytic (Fig. 22).

My observations agree with earlier reports on *S. bahamensis, S. clusiifolia, S. erythroxyloides,* and *S. sessiliflora* (Rothdauscher, 1896; Gaucher, 1902; Hayden, 1980).

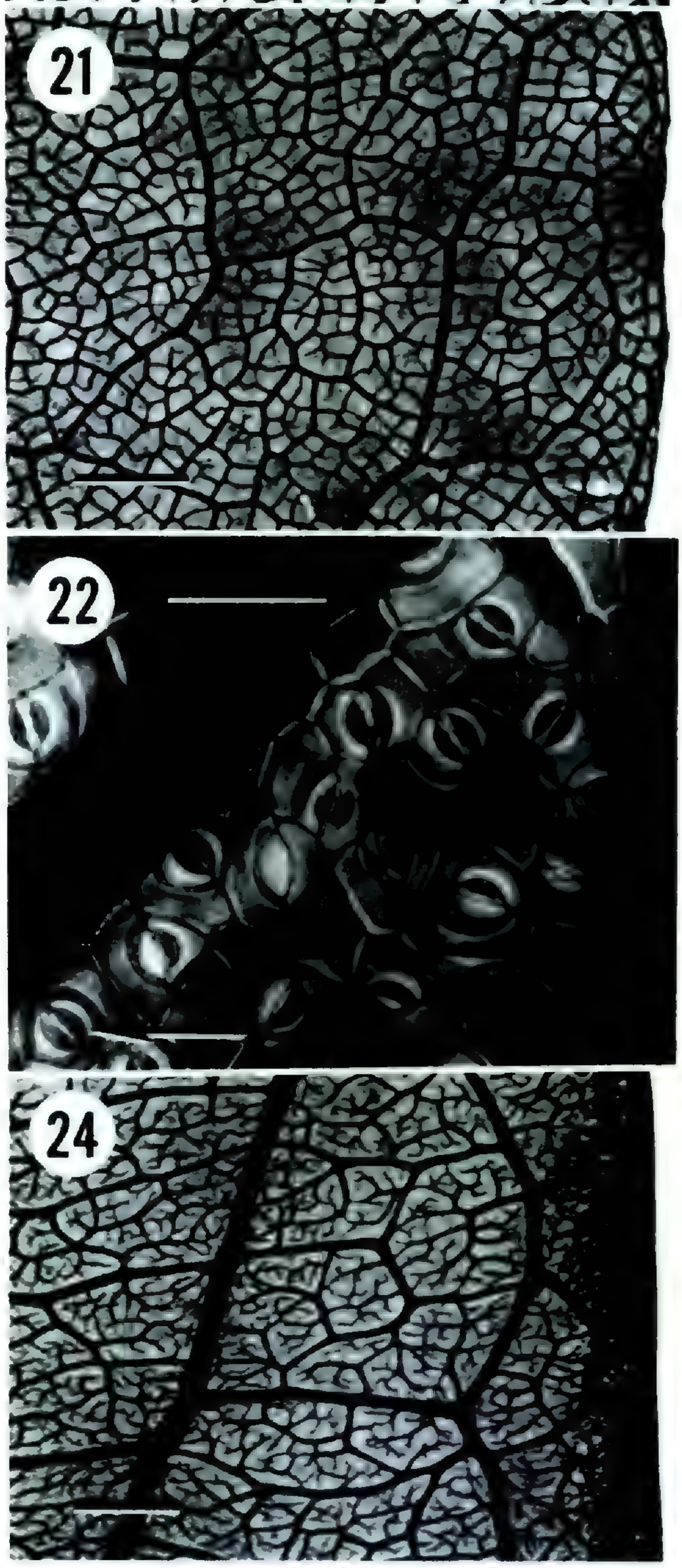
The leaves of the genera Webster placed in the Wielandieae generally form a homogeneous group. Two genera appear anomalous; however. *Astrocasia,* with its weakly percurrent tertiaries and narrow intercostal areas, appears more similar to some members of the Phyllantheae, a relationship suggested by both Punt (1962) and Köhler (1965) on the basis of pollen and even by Webster in an earlier paper (Webster, 1956). The leaves of *Pentrabrachium* are also of higher rank than typical of the Wielandieae, and further differ in the eucamptodromous secondaries, the presence of unicellular trichomes, and the undulate anticlinal walls of the epidermal cells. In these and other characters, *Pentabrachium* is much like *Dicoelia,* with which it shares the unusual condition of having the lower and medial secondaries eucamptodromous and the apical secondaries brochidodromous. Both phenetic and cladistic analyses of leaf characters suggest a close relationship between these genera (Levin, 1986 and in press), a possibility that has not been pro-







FIGURES 14–17. Leaves of *Pentabrachium* and *Petalodiscus*.—14, 15. *Pentabrachium reticulatum*.—16, 17. *Petalodiscus danguyana*. Bars equal 1 cm in Figures 14, 16 and 1 mm in Figures 15, 17.



FIGURES 18–24. Leaves of *Savia* and *Amanoa*.—18, 19. *Savia bahamensis*.—20, 21. *S. sessiliflora*.—22. *S. bahamensis*, abaxial epidermis, showing paracytic and parallelocytic (arrow) stomata.—23. *Amanoa oblongifolia*.—24. *A. guianensis*. Darkening of margin is due to sclerified epidermal cells. Bars equal 1 cm in Figures 18, 20, 23; 1 mm in Figures 19, 21, 24; and 50 μm in Figure 22.

TABLE 3. Epidermal characters in species of *Amanoa*.

Species	Cell Size Patterns		Sclerified Cells	
	Adaxial	Abaxial	Adaxial	Abaxial
glaucophylla	small cells in groups of 5–15 with matrix of large cells	small and large cells randomly mixed	dense near margin	scattered isolated cells and small groups of cells in intercostal areas; dense beneath low order veins and near margin
grandifolia	small and large cells randomly mixed	small and large cells randomly mixed	none or scattered near margin	scattered isolated cells and small groups of cells in intercostal areas; dense beneath low order veins and near margin
guianensis	small and large cells randomly mixed	two size classes not well differentiated	none or scattered near margin	few scattered isolated cells in intercostal areas; dense beneath low order veins and near margin
oblongifolia	only small cells present	only small cells present	scattered isolated cells in intercostal areas; dense over low order veins and near margin	almost all cells sclerified, except scattered groups in intercostal areas and stomatal cells

posed previously but that deserves further consideration.

Blotia, Petalodiscus, Savia, and *Discocarpus* appear to form a closely related group. A trend toward disorganization of the lower order venation coupled with increasing organization of the higher order venation, a very unusual pattern, can be traced from *Savia* sect. *Heterosavia* through sect. *Savia* to *Petalodiscus* and *Discocarpus. Blotia* is quite similar to *Savia,* differing mainly in the large size of its leaves.

AMANOEAE (PAX & HOFFM.) WEBST.

Amanoa Aubl. (OTU 10)

A. glaucophylla Muell. Arg., Guyana: Amazonas, *Krukoff 6370* (A). Figure 25.

A. grandifolia Muell. Arg., Venezuela: *Pittier 14799* (UC). Figures 26–28.

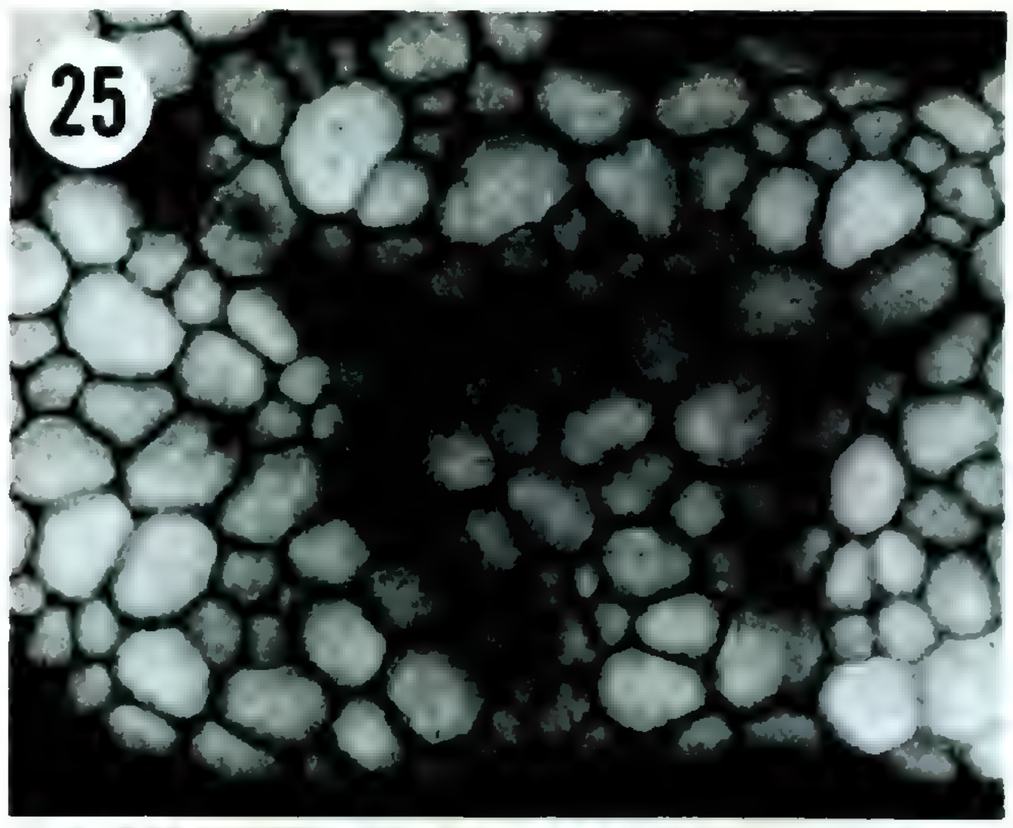
A. guianensis Aubl., Venezuela: *Cardona 401* (UC). Figure 24.

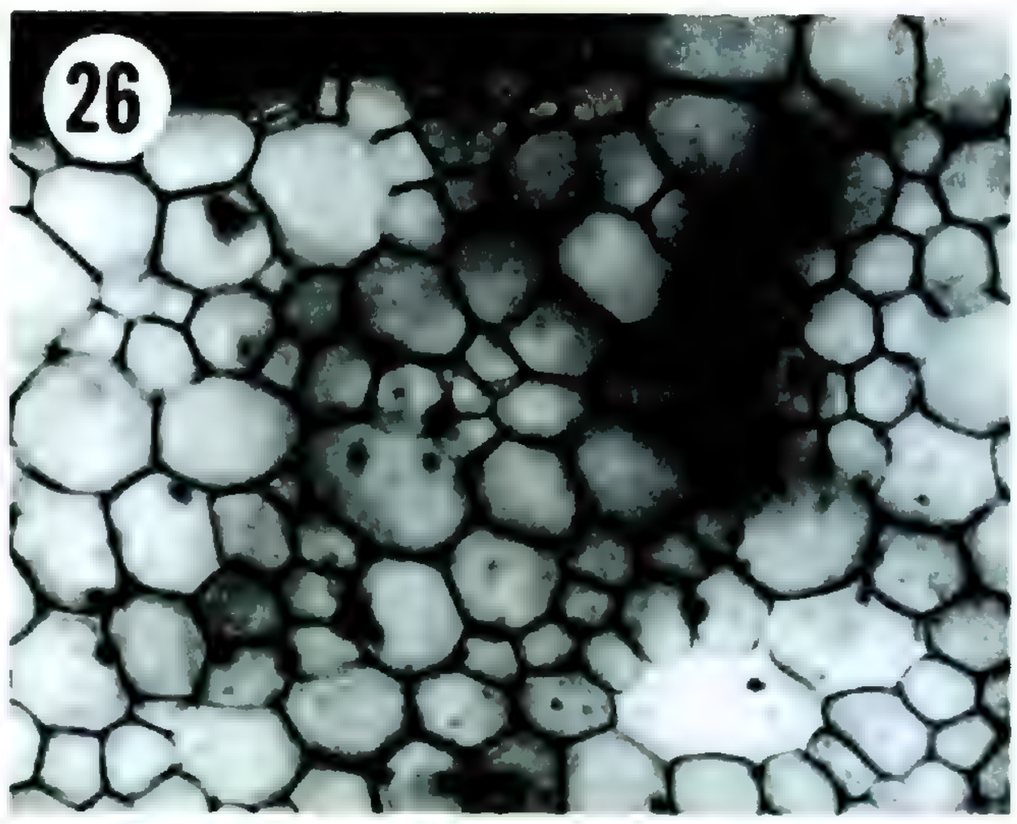
A. oblongifolia Muell. Art., Guyana: Amazonas, *Krukoff 7015* (A). Figures 23, 29, 30.

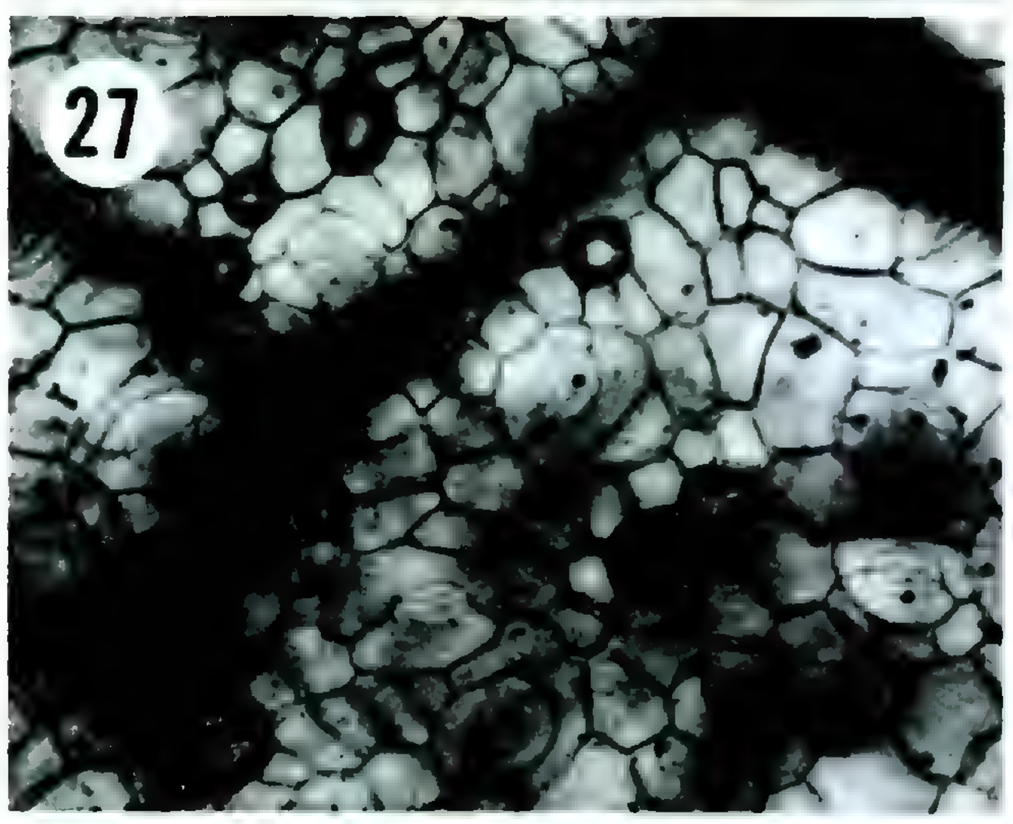
Leaves microphylls to mesophylls, symmetrical, oblong or elliptic; apex acuminate; base acute, obtuse, or rounded; organization of venation low third rank; marginal ultimate venation looped or weakly fimbriate; terminal tracheids normal to slightly enlarged; bundle sheath of higher order veins parenchymatous; stomata paracytic or rarely parallelocytic.

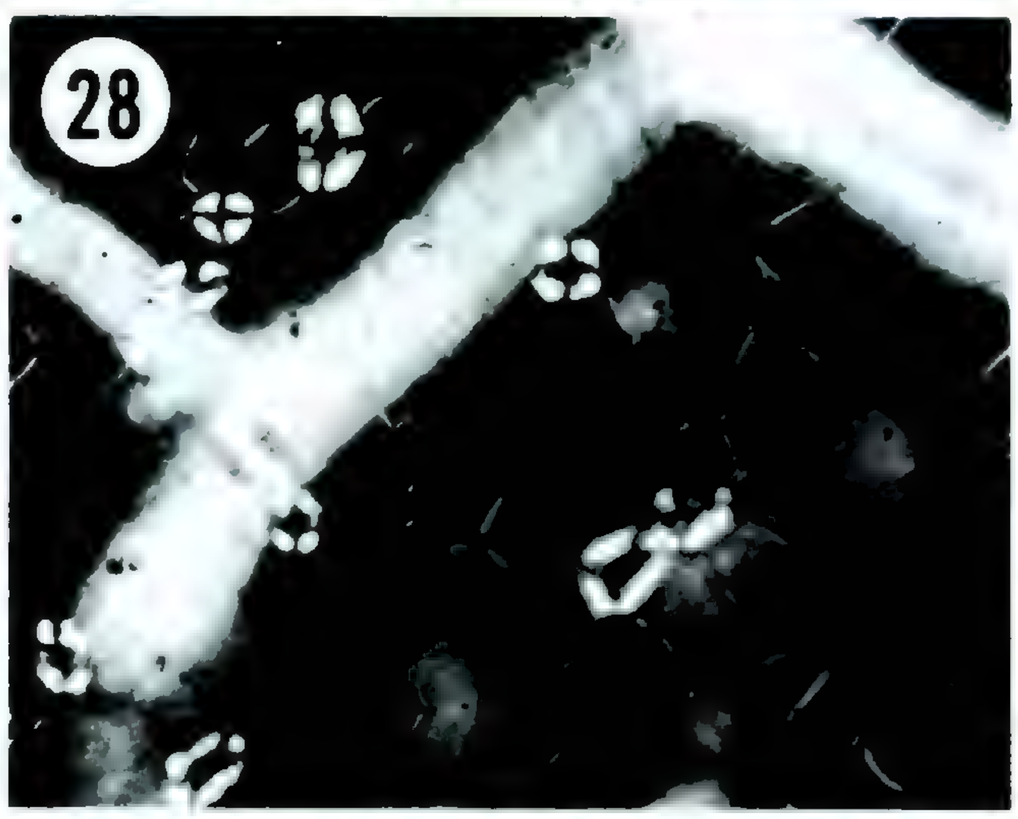
Of the seven to nine species in this genus, the leaves of only *A. glaucophylla* and *A. oblongifolia* have previously been described (Rothdauscher, 1896; Gaucher, 1902; Hayden, 1980). My observations agree with the earlier descriptions except for Rothdauscher's report, repeated by Metcalfe and Chalk (1950), of papillae and corkworts in the lower epidermis of *A. glaucophylla.* Reports of enlarged terminal tracheids vary in the literature. My observations suggest that this is a variable character within the genus, perhaps even within some of the species.

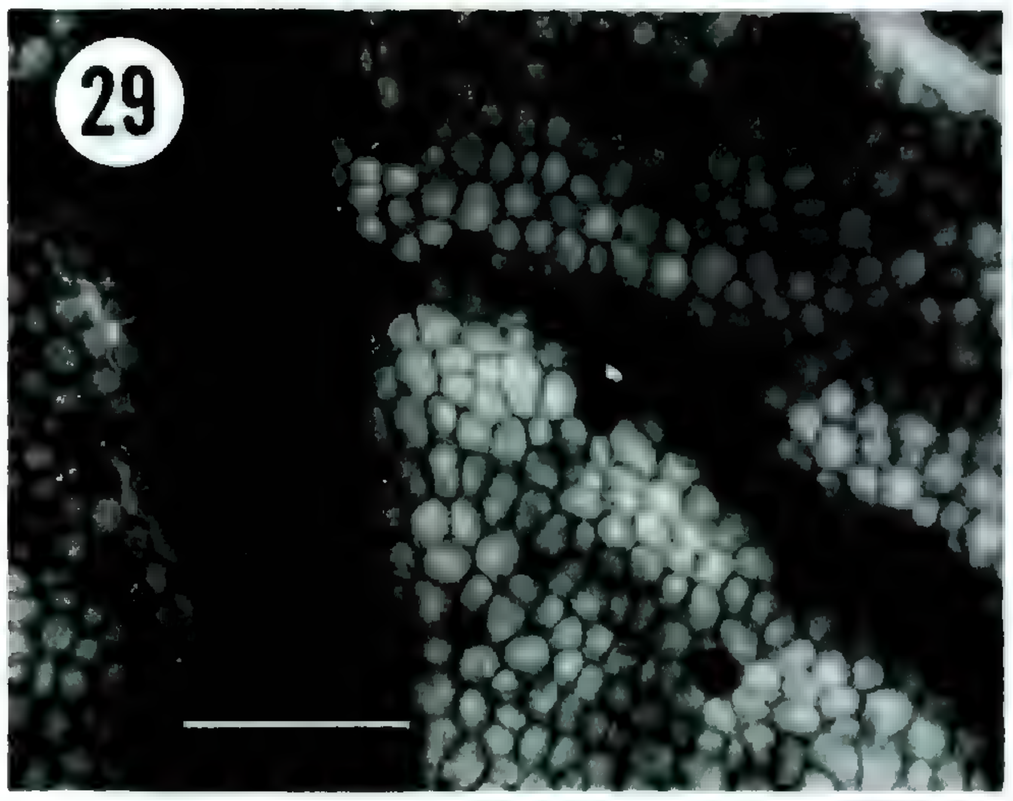
As observed by Rothdauscher, Gaucher, and Hayden, cells of the lower epidermis of *Amanoa* exhibit different patterns of sclerification. In addition, rather than being of relatively uniform size as in most phyllanthoids, the epidermal cells of most *Amanoa* species are of two sizes: larger cells with diameters of about 35 μm and smaller cells with diameters of about 16 μm. The distributions of cells of the two sizes vary from species to species. Table 3 details the distribution of large and small cells and sclerified cells in the four species I examined; some of the patterns are illustrated in Figures 25–30. The variation in these

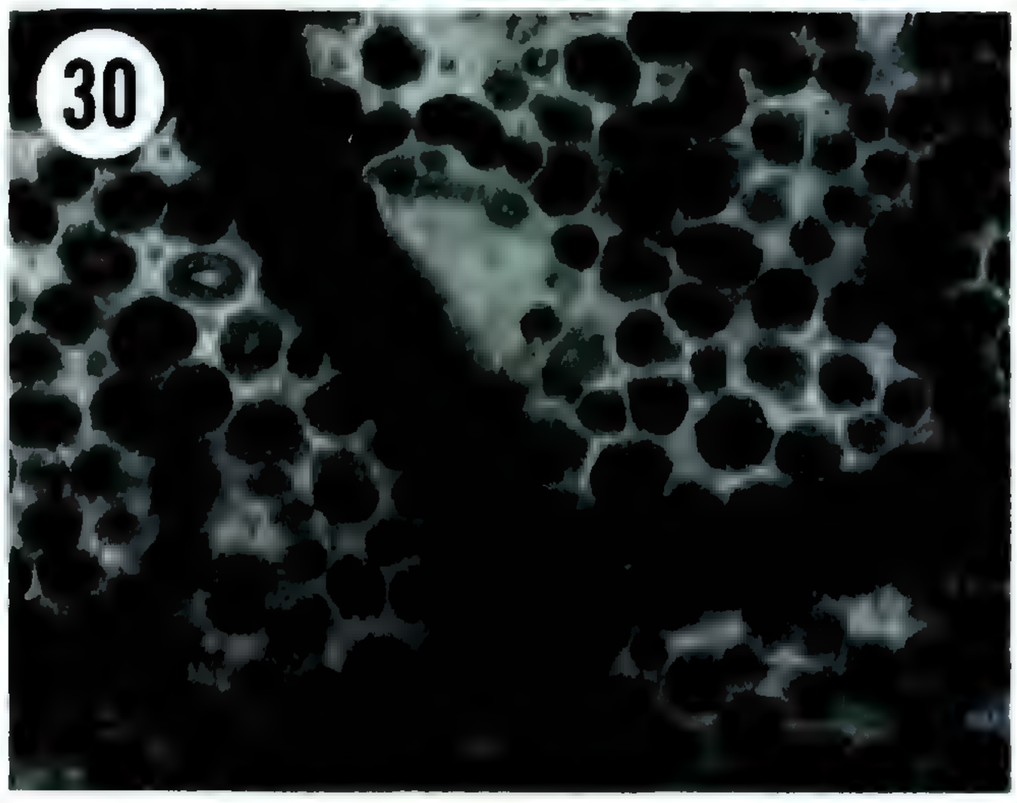












FIGURES 25–30. Epidermal cell patterns of *Amanoa*. Compare with Table 3.—25. *A. glaucophylla*, adaxial epidermis.—26. *A. grandifolia*, adaxial epidermis.—27, 28. *A. grandifolia*, abaxial epidermis, photographed with normal and polarized light, respectively. Sclerified cells are bright with polarized light.—29, 30. *A. oblongifolia*, adaxial and abaxial epidermis respectively. Bar equals 100 μm.

epidermal characters in the different species and the apparent constancy of the patterns within species suggest that the patterns may be useful in classification and identification.

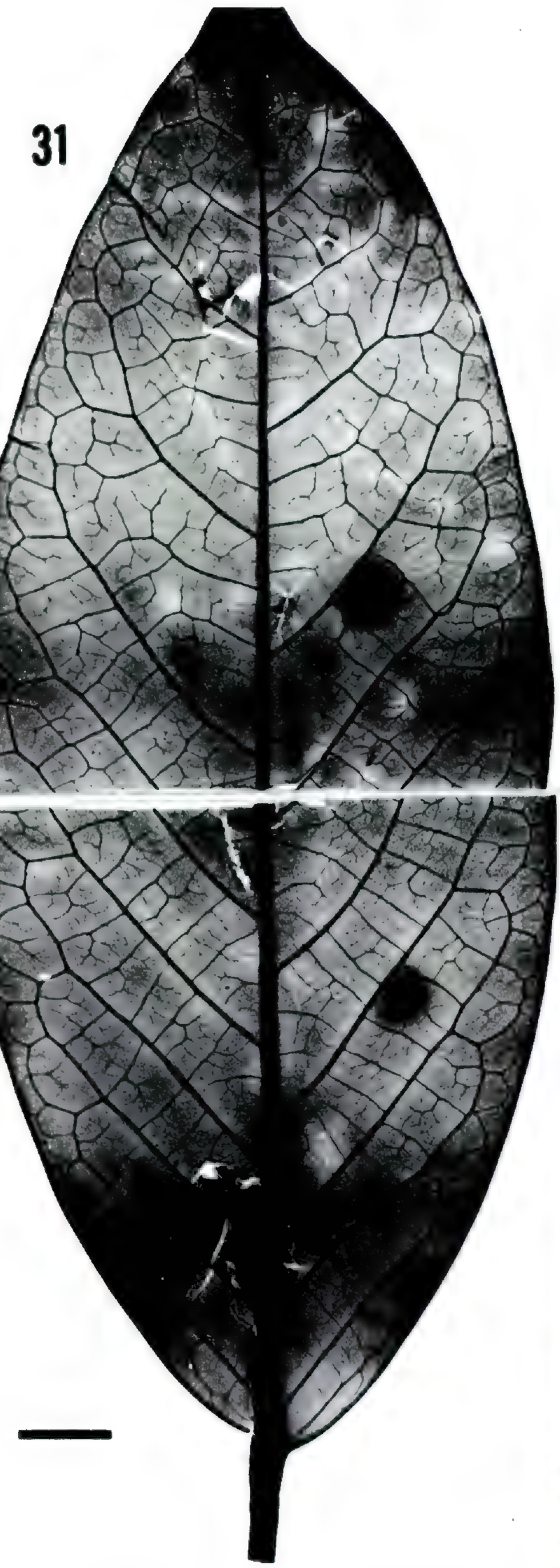
Actephila B1.

Group 1 (OTU 11)

A. anthelminthica Gagnep., Annam: *Poilane 9216* (UC).

A. nitidula Gagnep., Cochinchina: *Pierre (1907)* (UC). Figures 32, 33.

Leaves microphylls, symmetrical, narrow elliptic; apex acute; base acute-cuneate; organization of venation mid second rank; marginal ultimate venation incomplete (*A. anthelminthica*) or fimbriate (*A. nitidula*); terminal tracheids normal or slightly swollen; bundle sheath of higher order veins parenchymatous; stomata paracytic.



FIGURES 31–33. Leaves of *Actephila*.—31. *A. excelsa*.—32, 33. *A. nitidula*. Bars equal 1 cm in Figures 31, 32 and 1 mm in Figure 33.

Group 2 (OTU 12)

A. excelsa (Datz) Muell. Arg., Philippines: Mindanao, *Ramos & Edano 49158* (UC). Figure 31.

Leaves mesophylls, symmetrical, narrow ovate; apex acuminate; base rounded; organization of venation low third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes scattered on abaxial epidermis.

As Table 2 and the descriptions indicate, the leaves of *Actephila* form a very heterogeneous

group. Comparison with uncleared leaves of these and other species indicated that this variation is not an artifact of my small sample size; assessing the taxonomic significance of this variation requires study of cleared leaves from more species.

Croizatia Steyerm. (OTU 93)
C. naiguatensis Steyerm., Venezuela: *Tillett et al. 82* (DAV). Figures 34, 35.

Leaves mesophylls, symmetrical, elliptic; apex acute; base acute-decurrent; organization of venation low third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes scattered on abaxial epidermis and beneath midrib.

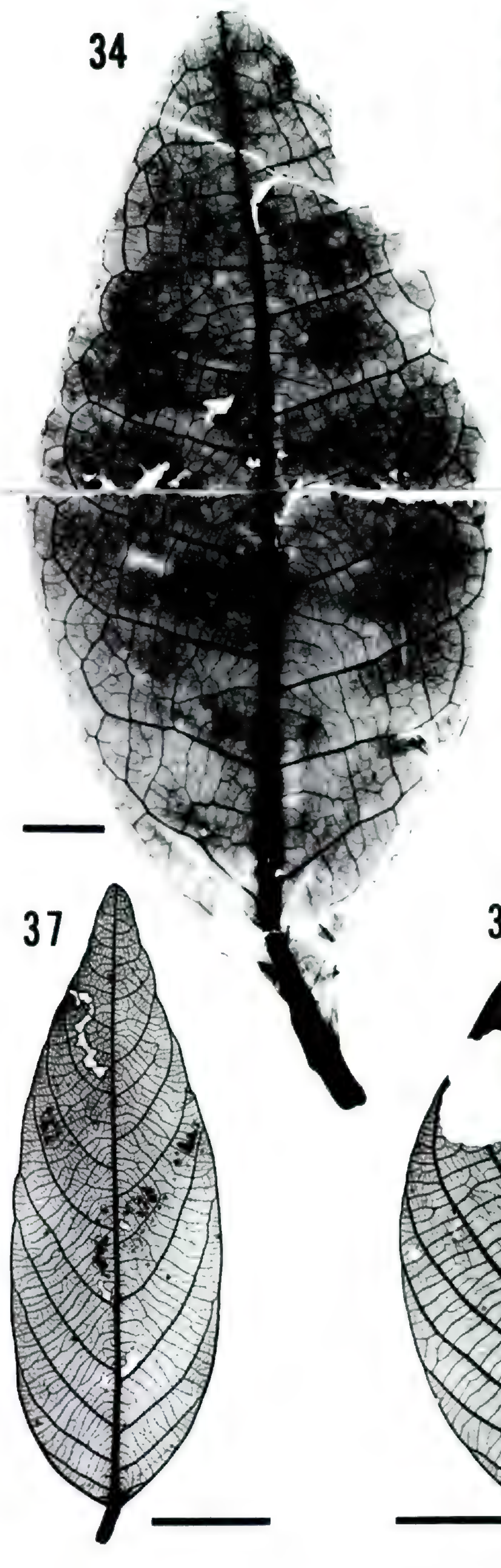
Although *Actephila* and *Amanoa* have traditionally been placed together, pollen of the two genera appears to be quite different (Punt, 1962; Köhler, 1965), as does the wood (Metcalfe & Chalk, 1950; Hayden, 1980). Leaf morphology does little to resolve the controversey. Cladistic and phenetic analyses of leaf characters place *Amanoa* near the Wielandieae, particularly *Wielandia, Blotia,* and *Savia* sect. *Heterosavia,* a position implied by Webster's classification and suggested by pollen and wood anatomy (Levin, 1986 and in press). The position of *Actephila* is less clear, largely due to the heterogeneity of its leaves. Leaves of *Actephila anthelminthica* and *A. nitidula* suggest a fairly close relationship to *Amanoa* and the Wielandieae, whereas the leaves of *A. excelsa* share more with the leaves of *Andrachne,* a relationship first proposed by Baillon (1858) and later supported by both Punt (1962) and Köhler (1965) on the basis of pollen. A relationship between *Actephila* and *Andrachne* is also more consistent with wood anatomy than is the association of *Actephila* and *Amanoa* (Metcalfe & Chalk, 1950; Hayden, 1980). Further study of leaves and other organs of *Actephila* will be necessary to clarify the relationships of this genus.

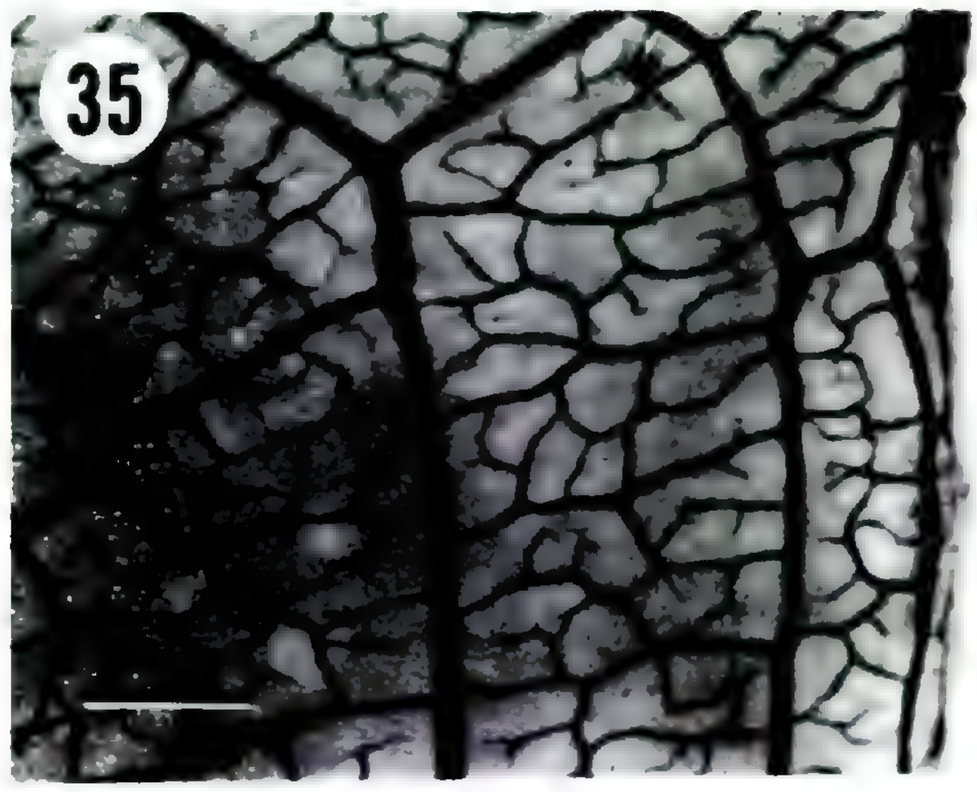
When Steyermark (1952) described *Croizatia,* he allied it with *Actephila* on the basis of strikingly similar fruits. Leaf morphology suggests a closer relationship to *Savia* and its relatives, particularly *Blotia.* More sampling within *Actephila* could conceivably turn up species more similar to *Croizatia* than the three I examined. Because male flowers of *Croizatia* remain unknown, the pollen has never been examined. We are similarly ignorant of most other aspects of the biology of this little known genus.

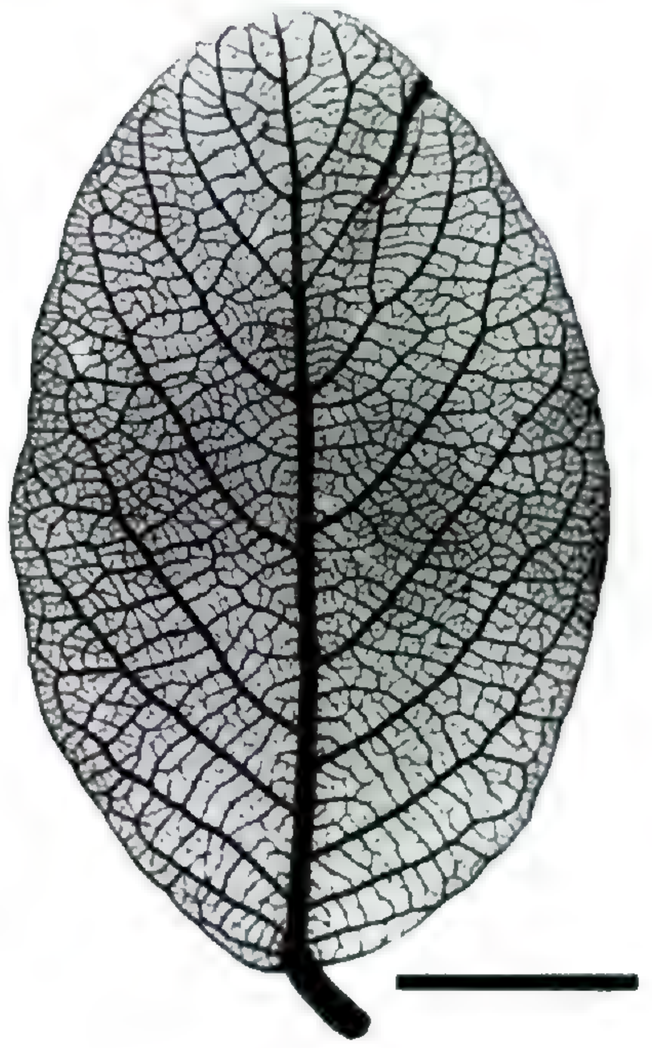
BRIDELIEAE MUELL. ARG.

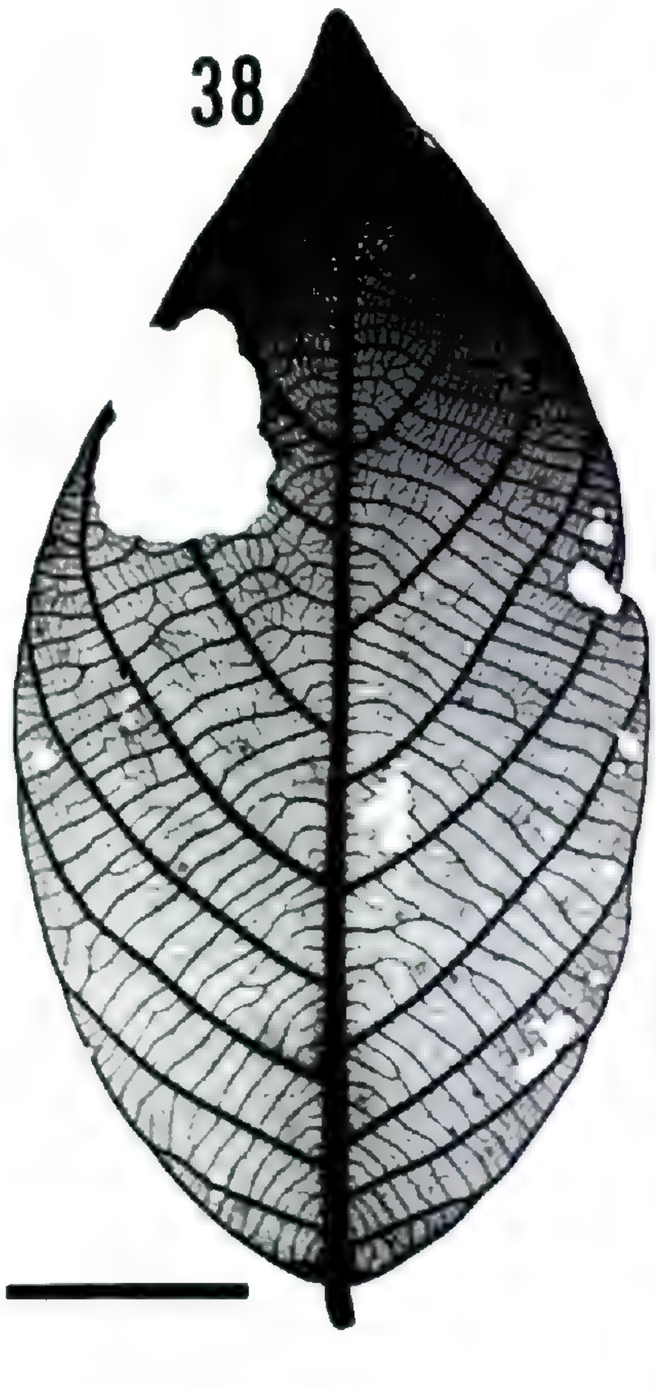
Bridelia Willd.
Group 1 (OTU 14)
Sect. *Micranthae* Gehrm.
B. atroviridis Muell. Arg., Cameroons: *Breteler 2866* (UC).
Sect. *Scleroneurae* Gehrm.
B. cathartica Bertol. f., Tanganyika: *Tanner 3541* (UC).
B. exaltata F. v. M., Australia: Queensland, *Kajewski 72* (UC). Figure 36.
B. mollis Hutch., Rhodesia: *Wormald (1951)* (UC).
Group 2 (OTU 15)
Sect. *Cleistanthoideae* Gehrm.
B. balansae Tutch., China: Kwangtung, *Chun 5982* (UC).
B. glauca Bl., Sumatra: *Boeea 7657* (UC). Figure 40.
B. minutiflora Hook. f., Philippines: *Ramos (1925)* (UC).
Group 3 (OTU 16)
Sect. *Micranthae* Gehrm.
B. glabrifolia (Muell. Arg.) Merr., Philippines: *Ramos & Edano (1924)* (UC). Figure 37.
B. micrantha (Hochst.) Baill., Ivory Coast: *de Wilde 452* (UC). Figure 39b.
Sect. *Scleroneurae* Gehrm.
B. monoica (Lour.) Merr., Sumatra: *Boeea 8440* (UC). Figures 38, 39a.
B. scleroneura Muell. Arg., Tanganyika: *Tanner 4160* (UC).
Sect. *Stipulares* Gehrm.
B. stipularis (L.) Bl., Sumatra: *Boeea 8275* (UC).

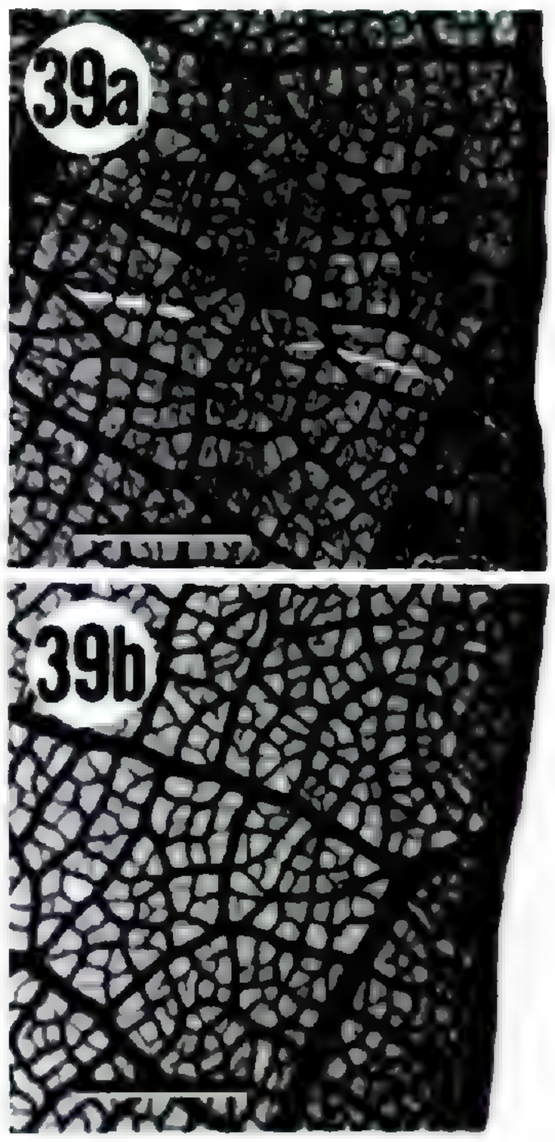
Leaves microphylls or mesophylls, symmetrical, ovate, elliptic, or obovate; apex acuminate, acute, obtuse, or rounded; base acute, obtuse, rounded, or cordate; organization of venation high third rank; marginal ultimate venation fimbriate or consisting of an intramarginal vein formed by the stiffening of the brochidodromous loops (see below); terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic, rarely one of the subsidiary cells divided by an additional wall perpendicular to the guard cells; trichomes typically at least beneath low order veins, may also











FIGURES 34–39. Leaves of *Croizatia* and *Bridelia*.—34, 35. *Croizatia naiguatensis*.—36. *Bridelia exaltata*.—37. *B. glabrifolia*.—38, 39a. *B. monoica*.—39b. *B. micrantha*. Bars equal 1 cm in Figures 34, 36–38 and 1 mm in Figures 35, 39a, b.

be scattered on abaxial or less commonly adaxial surfaces, rarely the leaves glabrous.

Gaucher (1902) reported sclerified bundle sheaths in *B. micrantha, B. obtusa,* and *B. zenkeri.*

Although all the species of *Bridelia* I examined are identified easily by their numerous secondaries and closely spaced, regularly and strongly percurrent tertiaries, three groups of species can be recognized on the basis of the patterns formed by the outer portion of the secondaries and the marginal ultimate venation. The first group, which includes some members of sects. *Micranthae* and *Scleroneurae,* has weakly brochidodromous secondaries and fimbriate marginal ultimate venation (Fig. 36). The second group, all members of sect. *Cleistanthoideae,* also has a fimbrial vein, but the secondaries are eucamptodromous (Fig. 40). In the third group, the secondary veins are brochidodromous with the outer portions of the loops forming an intramarginal vein. Close examination reveals that in some species, members of sects. *Stipulares* and *Scleroneurae,* the loops join without any abrupt change of direction (Figs. 38, 39a), whereas in other species, members of sect. *Micranthae,* each secondary vein bends sharply exmedially within 1 mm or less of joining the intramarginal vein (Figs. 37, 39b). As both *Micranthae* and *Scleroneurae* also contain species with the first leaf type, this difference may reflect independent origin of the intramarginal vein in the two sections. Resolving this and the question of the relationship of the eucamptodromous *Cleistanthoideae* awaits study of more species in this genus of over 60 species.

FIGURE 40. Leaf of *Bridelia glauca.* Bar equals 1 cm.

Cleistanthus Hook. f. ex Planch.

Group 1 (OTU 17)

C. acuminatissimus Merr., British N Borneo: *Elmer 21153* (UC). Figures 41, 42.

Group 2 (OTU 18)

Sect. *Stipulati* Jabl.

C. bridelifolius C. B. Rob., Sarawak: *Chew Wee-Lek 558* (UC).

C. siamensis Craib, Annam: *Poilane 5186* (UC).

Group 3 (OTU 19)

Sect. *Ferruginosi* Jabl.

C. barrosii Merr., Philippines: *Clemens 16870* (UC). Figure 43.

C. ferrugineus Muell. Arg., Ceylon: *Galston 2233* (UC).

Sect. *Pedicellati* Jabl.

C. integer C. B. Rob., Philippines: *Loger 12372* (UC), *Ramos & Edano (1926)* (UC).

Group 4 (OTU 20)

Sect. *Chartacei* Jabl.

C. cunninghamii Muell. Arg., Australia: Queensland, *Clemens (1944)* (UC).

Group 5 (OTU 21)

Sect. *Cleistanthus*

C. polystachyus Hook. f. ex Planch., Ivory Coast: *Leeuwenberg 3736* (UC).

Group 6 (OTU 22)

C. saichikii Merr., China: Hainan, *Lau 15* (UC).

Group 7 (OTU 23)

Sect. *Australes* Jabl.

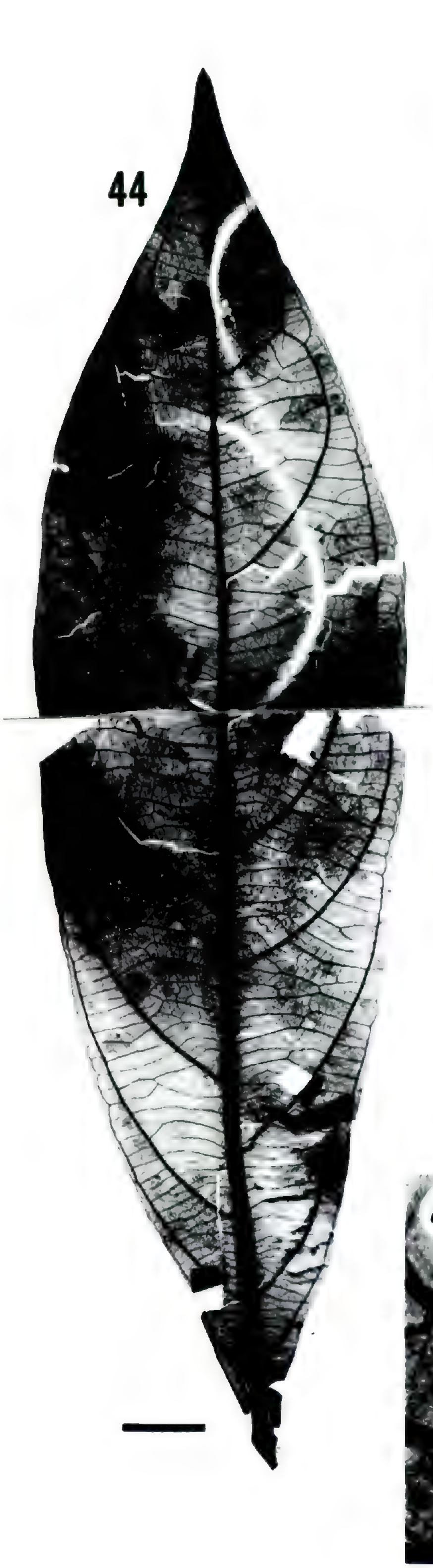
C. micranthus Croizat, Fiji: *Smith 9531* (UC).

Group 8 (OTU 24)

Sect. *Leiopyxis* (Miq.) Jabl.

C. apodus Bth., Australia: Queensland, *Irvine 670* (DAV).

C. blancoi Rolfe, Philippines: *Ramos & Edano* 1928 (UC).



FIGURES 41–46. Leaves of *Cleistanthus, Dicoelia,* and *Poranthera.*—41, 42. *Cleistanthus acuminatissimus.*—43. Dolabrate trichome of *C. barrosii.*—44. *Dicoelia affinis.*—45. Filiform sclereids of *D. affinis.*—46. *Poranthera corymbosa.* Bars equal 1 cm in Figures 41, 44; 1 mm in Figures 42, 46; and 100 μm in Figures 43, 45.

C. ripicolus Leonard, Nigeria: *Onochie FHI 33213* (DAV).

Leaves microphylls or mesophylls, symmetrical, typically narrow elliptic or lanceolate; apex acute or acuminate; base acute, obtuse, or rounded; organization of venation typically low to mid third rank, rarely (*C. micranthus*) second rank; marginal ultimate venation fimbriate or rarely looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic or brachyparacytic; leaves glabrous or with trichomes scattered abaxially.

Two features unusual in the Phyllanthoideae appear in some *Cleistanthus* species. Members of sects. *Chartacei, Cleistanthus,* and *Leiopyxus* have a network of filiform fibers in the mesophyll giving the veins a frayed appearance. Only *Dicoelia* has similar fibers. Unique in the Phyllanthoideae are the two-armed dolabrate trichomes (Fig. 43) borne by species of sects. *Chartacei* and *Ferruginosi.*

Overall, most species of *Cleistanthus* included in this study are quite similar. The exceptions are the only representatives of sects. *Chartacei* (*C. cunninghamii*) and *Australes* (*C. micranthus*) that I examined. Both have strongly brochidodromous secondaries arising at higher angles than typical for the genus and less well organized higher order venation than most of the other species. The latter is particularly true of *C. micranthus* in which the tertiary veins are random reticulate rather than percurrent. The leaves of *C. cunninghamii* are not typical of *Chartacei* (Jablonsky, 1915); it is unfortunate that this is the only species in the section that I was able to obtain. On the basis of non-foliar characters, Jablonsky (1915) felt that *Australes* were rather isolated in *Cleistanthus,* which is corroborated by my evaluation of the leaves.

Typical leaves of the two genera in the Bridelieae do not seem to resemble each other very closely, but a connection between them can be seen through some of the higher ranked species of *Cleistanthus* and the fimbrial-veined groups of *Bridelia,* in agreement with the general interpretation, based on floral characters, that *Bridelia* is derived from *Cleistanthus*-like ancestry. After studying pollen exine sculpturing of four species each of *Bridelia* and *Cleistanthus,* Köhler (1965) suggested that *Bridelia* was derived polyphyletically from *Cleistanthus.* Examination of the pollen and leaves of more species in both genera might help clarify the relationship between them.

DICOELIEAE HURUSAWA

Dicoelia Benth. (OTU 25)
D. affinis J. J. Sm., Borneo: *Hallier 1255* (UC). Figures 44, 45.

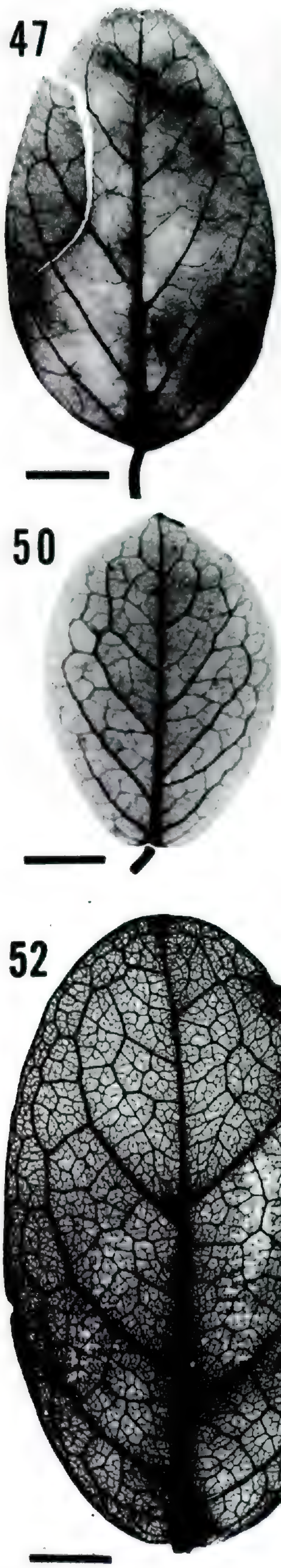
Leaves mesophylls, symmetrical, narrow elliptic; apex acuminate; base acute-cuneate; organization of venation third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes scattered on abaxial epidermis.

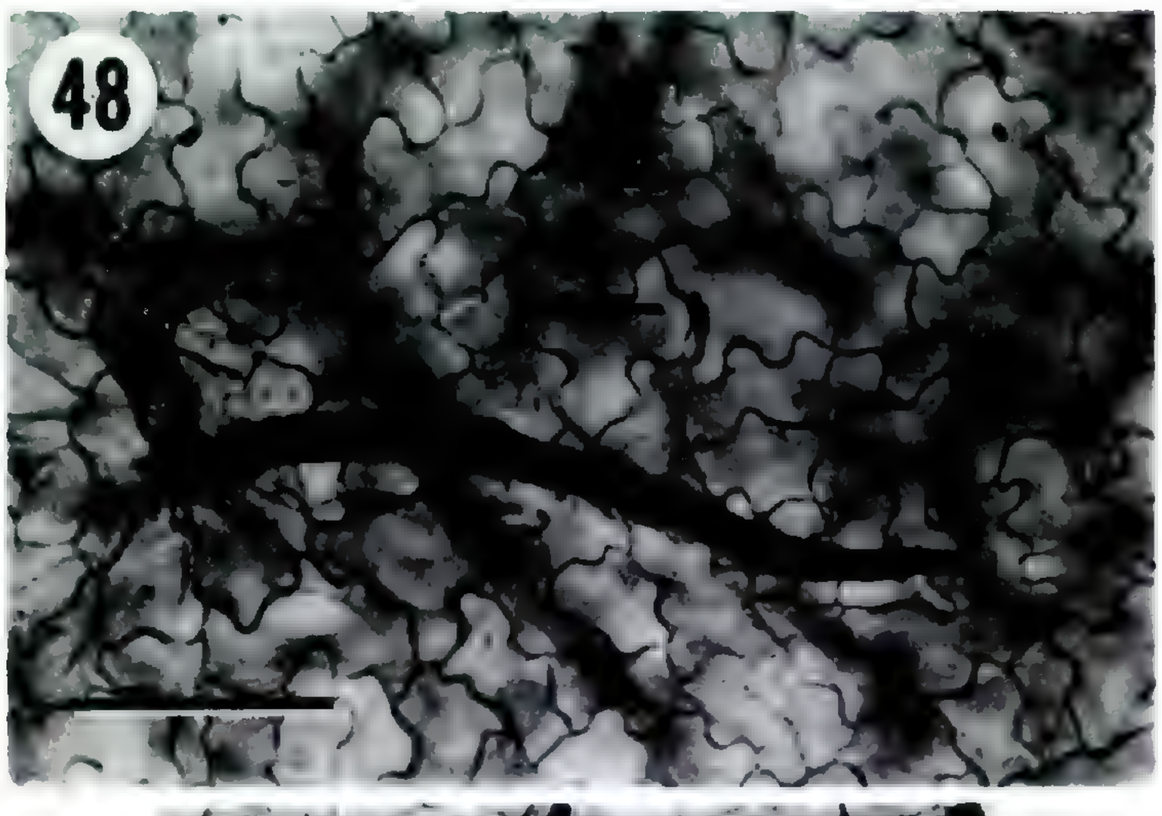
The leaves of *Dicoelia* share with some *Cleistanthus* species having filiform fibers in the mesophyll (Fig. 45). In general, however, the resemblance between these genera is not strong, which is consistent with the evidence from pollen morphology (Punt, 1962; Köhler, 1965) and wood anatomy (Metcalfe & Chalk, 1950). Indeed, as discussed above, foliar morphology suggests a relationship between *Dicoelia* and *Pentabrachium,* a relationship not before considered.

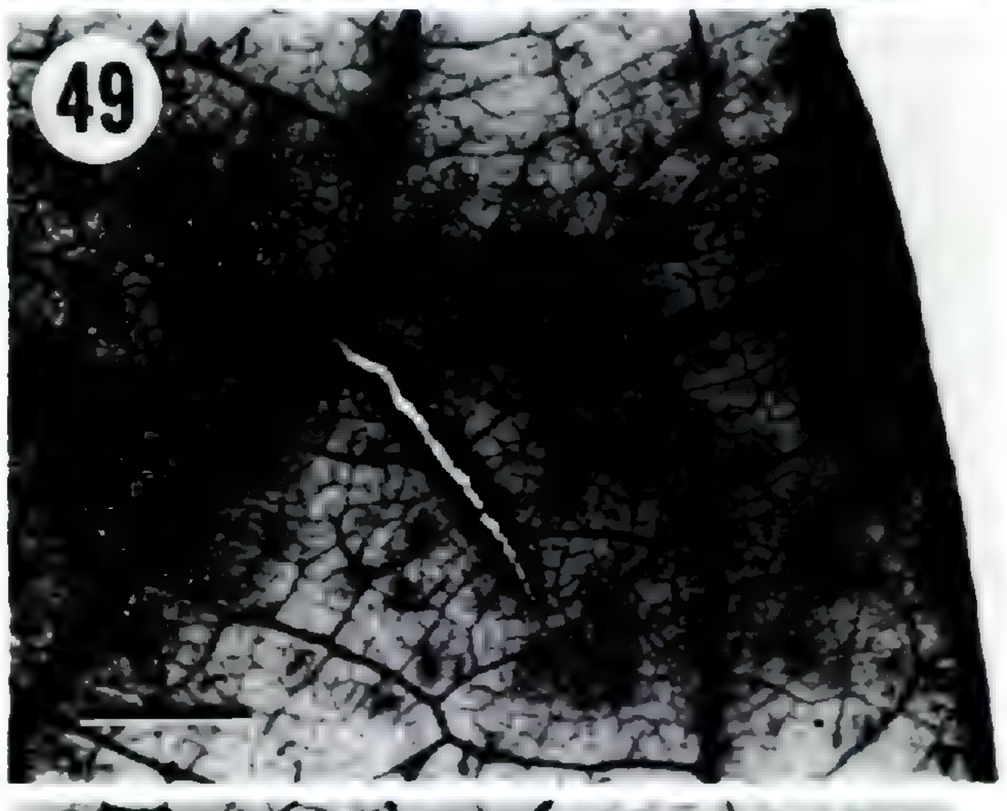
PORANTHEREAE (MUELL. ARG.) GRUNIG

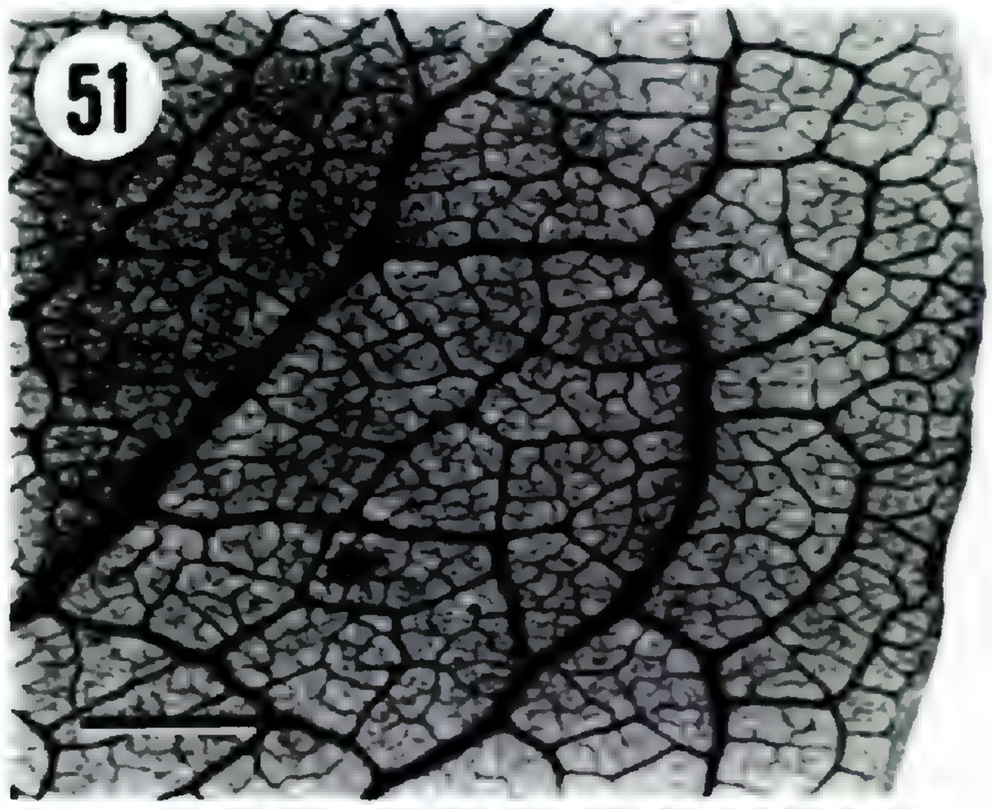
Poranthera Rudge.
P. corymbosa Brongn., Australia: New South Wales, *Boorman (1903)* (UC). Figure 46.

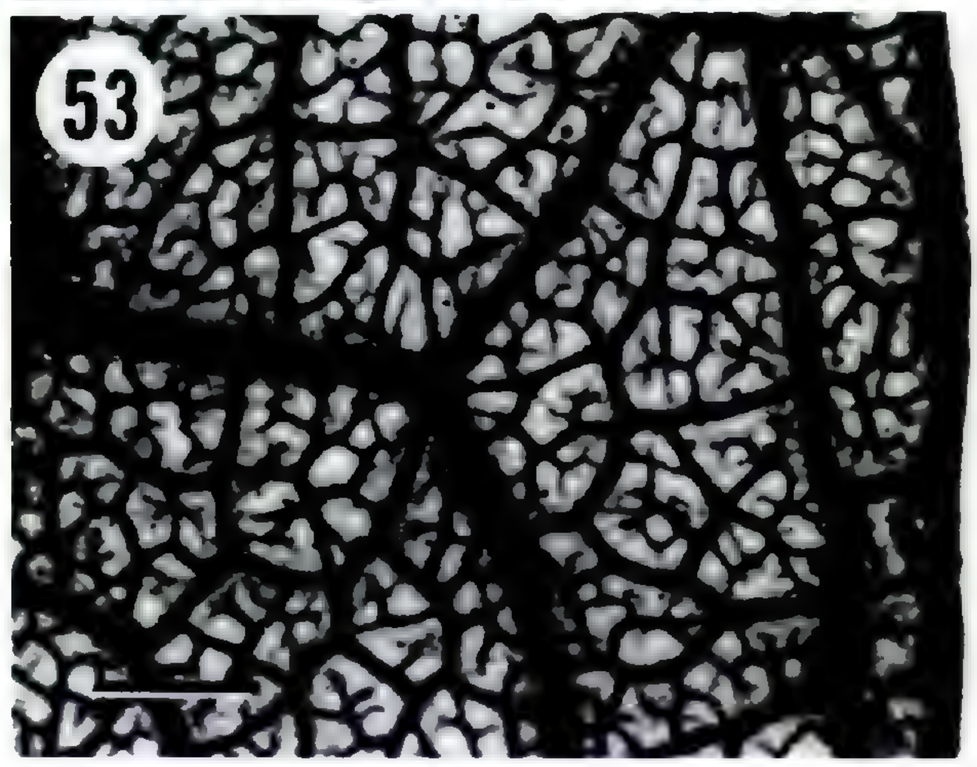
Leaves simple, sessile, nanophylls, symmetrical, linear; apex acute; base symmetrical, the margins parallel; margin revolute; organization of venation low first rank, pinnate, kladodromous; primary vein massive, straight; secondary vein angle of origin very narrow acute and more or less uniform, thickness moderate to fine, course zig-zag and branched; higher vein orders not well resolved, forming an irregular reticulum of gradually thinning veins; marginal ultimate venation looped; areoles large and extremely irregular in size and shape; veinlets irregularly branched; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; adaxial epidermal cells rectangular, abaxial cells isodiametric, both arranged randomly, anticlinal walls undulate, abaxial cells with thickened ridges on the undulations, surfaces smooth; stomata abaxial, orientation random, stomatal index about 20%, brachyparacytic, the guard cells sunken and almost obscured by the subsidiary cells; trichomes and crystals none.











FIGURES 47–53. Leaves of *Andrachne* and *Spondianthus*.—47. *Andrachne chinense*.—48. Abaxial epidermis of *A. chinense*, showing unicellular trichome and anisocytic stomata (arrow).—49. *A. australis*.—50, 51. *A. phyllanthoides*.—52, 53. *Spondianthus preussii*. Bars equal 1 cm in Figures 47, 52; 5 mm in Figure 50; 1 mm in Figures 49, 51, 53; and 100 μm in Figure 48.

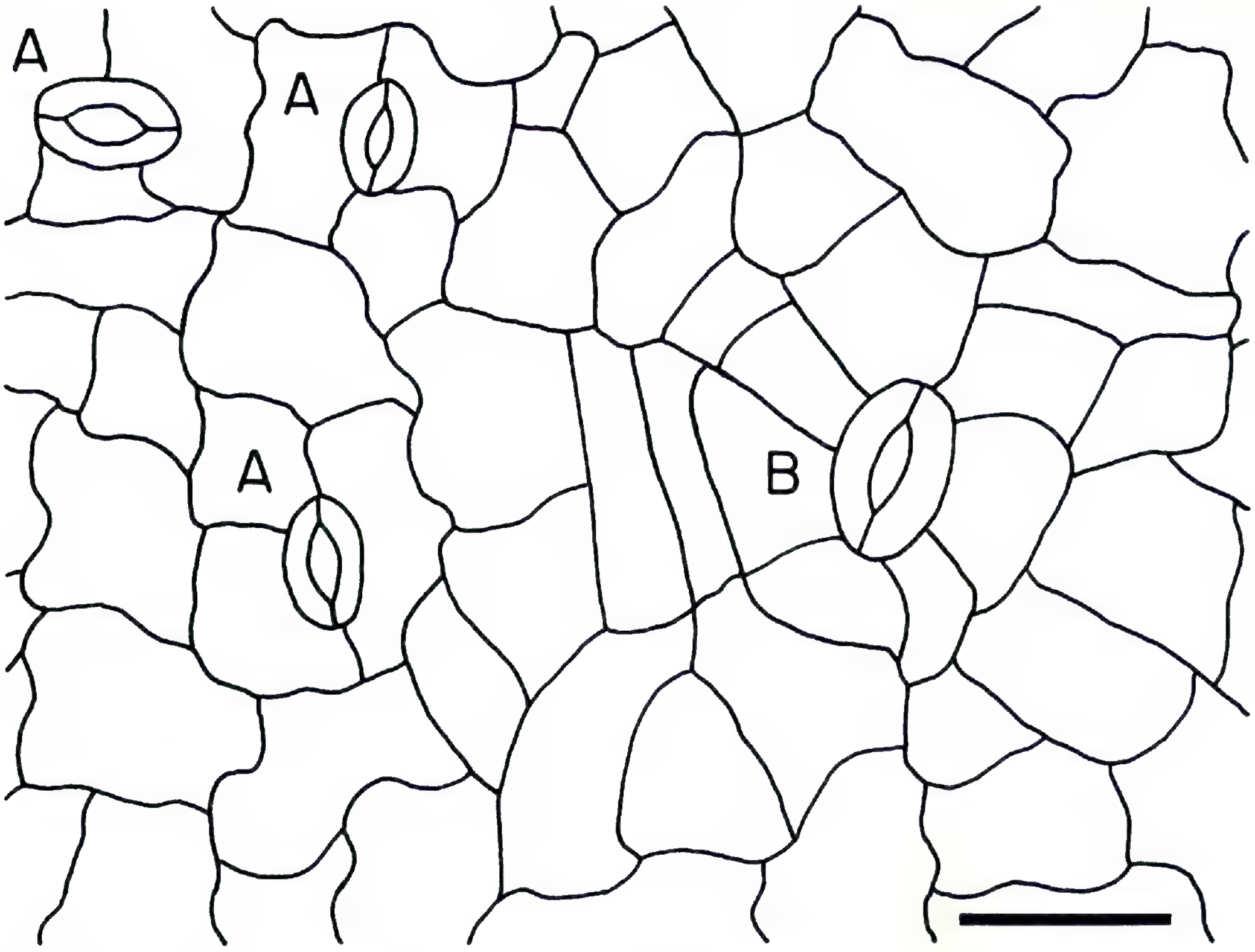


FIGURE 54. Abaxial epidermis of *Andrachne chinense*, showing anisocytic (A) and large anomocytic (B) stomata. Bar equals 100 μm.

Andrachne L.

Group 1 (OTU 26)

Sect. *Arachne* (Neck.) Endl.

A. australis Zoll., Annam: *Poilane 4755* (UC). Figure 49.

A. chinense Bunge, India: Punjab, *Koelz 4423* (UC). Figures 47, 48, 54.

A. cordifolia Muell. Arg., Pakistan: *Rodin 5378* (UC).

Sect. *Phyllanthidia* (Didrichs.) Muell. Arg.

A. microphylla (Lam.) Baill., Peru: *Sagastegni & Cabanillas 8738* (DAV).

Leaves microphylls, symmetrical, ovate; apex attenuate or rounded to emarginate; base acute, obtuse, or rounded; organization of venation high second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; typical stomata anisocytic (Fig. 48), large anomocytic "water stomata" also present (Fig. 54); trichomes scattered on abaxial epidermis, denser beneath lower order veins, in some species also scattered on adaxial epidermis.

Group 2 (OTU 27)

Sect. *Phyllanthopsis* (Scheele) Muell. Arg.

A. arida (Warnock & M. C. Johnst.) Webster, U.S.A.: Texas, *Butterwick & Lott 3582* (DAV).

A. phyllanthoides (Nutt.) Muell. Arg., U.S.A.: Missouri, *Palmer 45338* (UC). Figures 50, 51.

Leaves nanophylls, symmetrical, elliptic; apex obtuse; base acute or rounded; organization of venation low second rank; marginal ultimate venation looped (*A. phyllanthoides*) or incomplete (*A. arida*); terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata anisocytic; trichomes scattered on both surfaces, densest beneath midrib and secondaries.

My anatomical observations generally agree with those of Rothdauscher (1896), who included *A. chinensis, A. cordifolia,* and *A. phyllanthoides* among the seven species he studied. He did not, however, report the large anomocytic stomata I found in sects. *Arachne* and *Phyllanthidia*.

The members of this tribe are perennial herbs or subshrubs, many extending into drier and more temperate habitats than most other phyllanthoids (Pax & Hoffmann, 1922; Webster, 1967). Surprisingly, the rank of the venation of the two species in *Andrachne* sect. *Phyllanthopsis* remains comparatively high for such xeromorphic leaves, which generally show a regression in organization below the leaves of their more mesophytic relatives (Hickey, 1971). The strikingly low rank of the leaves of *Poranthera* reflects the extremely xerophytic nature of this Australian endemic and reveals nothing about its relationships.

Section *Phyllanthopsis* has been repeatedly transferred between *Savia* and *Andrachne* (cf. Mueller, 1866; Pax & Hoffmann, 1922; Webster, 1967). The anisocytic stomata and undulate anticlinal walls on the epidermal cells suggest that *Phyllanthopsis* is better included in *Andrachne,* the conclusion both Punt (1962) and Köhler (1965) came to when studying the pollen. The venation of *Phyllanthopsis* also appears somewhat more organized than would be expected from a xeric *Savia* derivative, being more comparable to other *Andrachne* sections.

SPONDIANTHEAE WEBST.

Spondianthus Engl. (OTU 28)

S. preussii Engl., Cameroons: *Zenker 563* (CAS), Ghana: *Oldeman 818* (MO), Congo: *Louis 13728* (UC). Figures 52, 53.

Leaves mesophylls, symmetrical, wide elliptic; apex rounded; base rounded; organization of venation second rank; marginal ultimate venation fimbriate; terminal tracheids normal; bundle sheath of higher order veins sclerified; stomata paracytic.

The paracytic stomata and tanniniferous epidermal cells would associate *Spondianthus* with the Antidesmeae, in which the second rank venation, few secondaries enclosing large intercostal areas, and random-reticulate tertiaries with a tendency to ramify admedially would be anomalously primitive. I am inclined to agree with Webster's (1975) placement of this genus in its own tribe near the Antidesmeae, of which it may be the primitive sister group (Levin, in press).

ANTIDESMEAE (ENDL.) HURUSAWA

Antidesma L.

Group 1 (OTU 29)

Sect. *Roxburghiana* Pax & K. Hoffm.

A. vogelianum Muell. Arg., Tanganyika: *Tanner 2564* (UC).

Sect. *Venosa* Pax & K. Hoffm.

A. henryi Hemsl., China: Hainan, *Tsang et al. 23* (UC).

A. japonicum Sieb. & Zucc., Taiwan: *Tanaaka & Shimada 13570* (UC).

A. venosum Tul., Tanganyika: *Tanner 3424* (UC). Figure 55.

Group 2 (OTU 30)

Sect. *Laciniata* Pax & K. Hoffm.

A. laciniatum Muell. Arg., Congo: *Louis 11467* (MO).

Sect. *Venosa* Pax & K. Hoffm.

A. cuspidatum Muell. Arg., Sumatra: *Toroes 5296* (UC).

A. delicatulum Hutch., China: Chekiang, *Ching 2038* (CU). Figures 57, 58.

A. gracile Hemsl., China: Kwangtung, *Tsang 21272* (UC).

A. maclurei Merr., China: Hainan, *Fung 20210* (UC).

A. membranaceum Muell. Arg., Belgian Congo: *Louis 6088* (UC), Ghana: *Hall & Abbiw 43391* (GC).

Group 3 (OTU 31)

Sect. *Tetrandra* Pax & K. Hoffm.

A. angusanense Elm., Philippines: *Ramos & Pasgasio (1919)* (UC).

A. digitaliforme Tul., Philippines: *McClure 15967* (UC).

A. fructifera Elm., Philippines: *Ramos (1915)* (UC). Figure 56.

Group 4 (OTU 32)

Sect. *Montana* Pax & K. Hoffm.

A. bunius Spreng., China: Kwangtung, *Tsiang Ying 1013* (UC).

A. insulare Gillespie, Fiji: *Smith 656* (UC).

A. platyphyllum Mann, U.S.A.: Hawaii, *Meinecke (1933)* (UC).

Group 5 (OTU 33)

Sect. *Velutinosa* Pax & K. Hoffm.

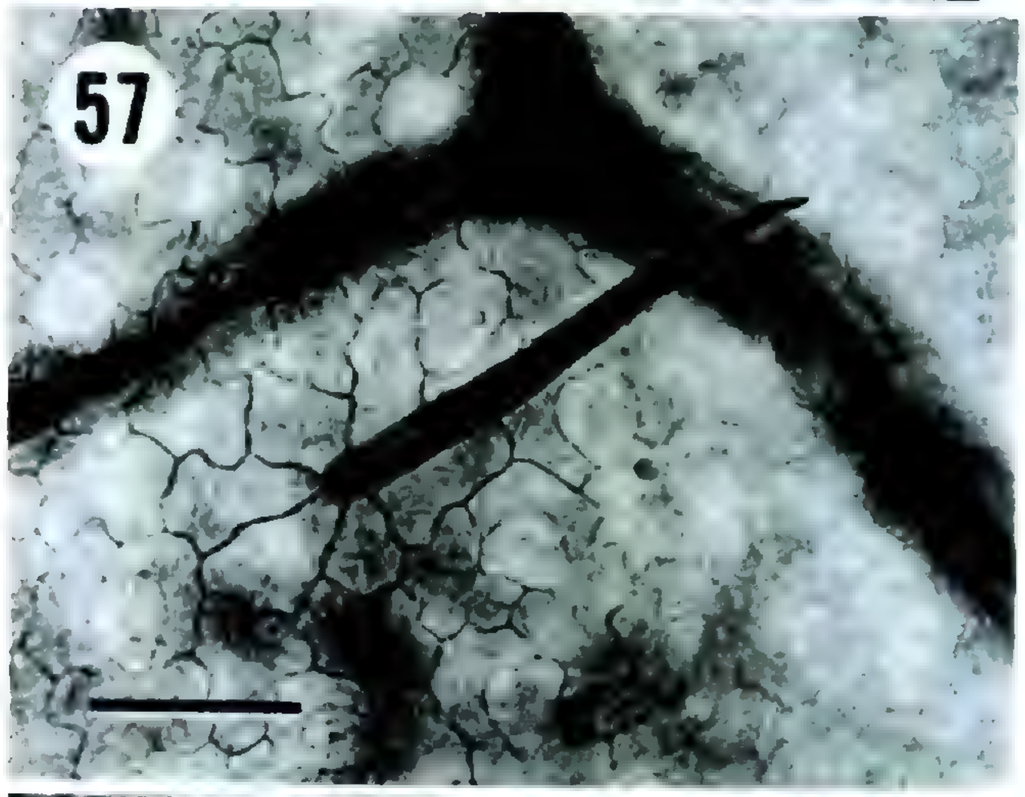
A. fordii Hemsl., Hong Kong: *Chun 5089* (UC).

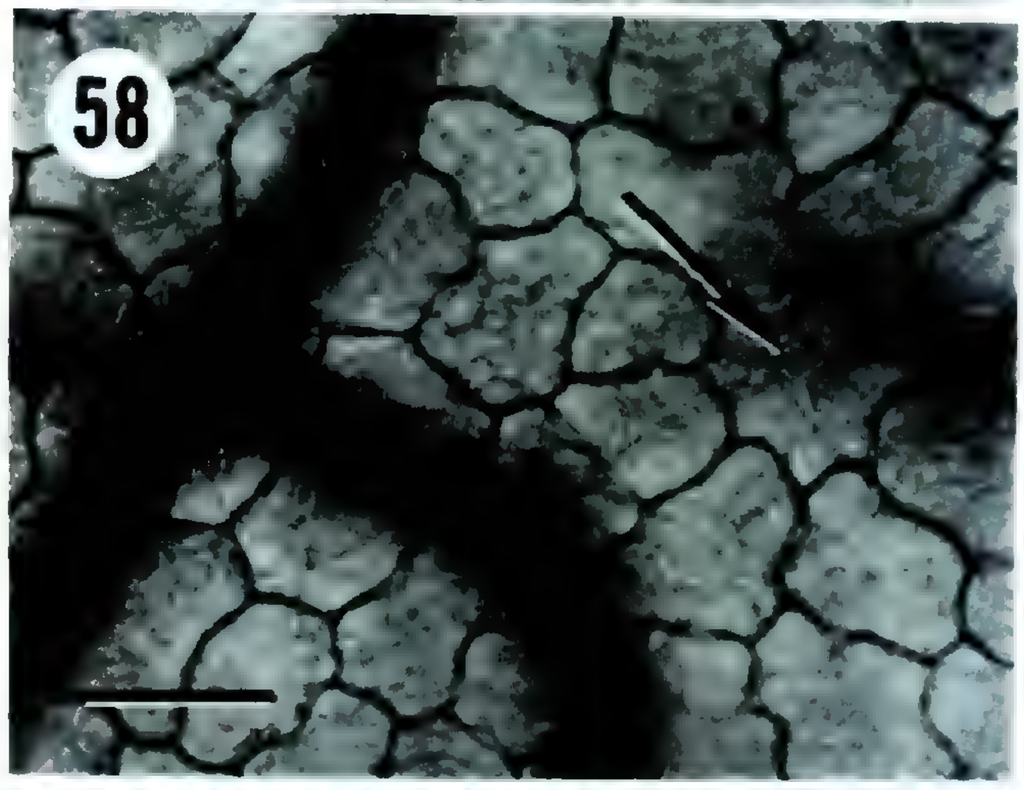
Group 6 (OTU 34)

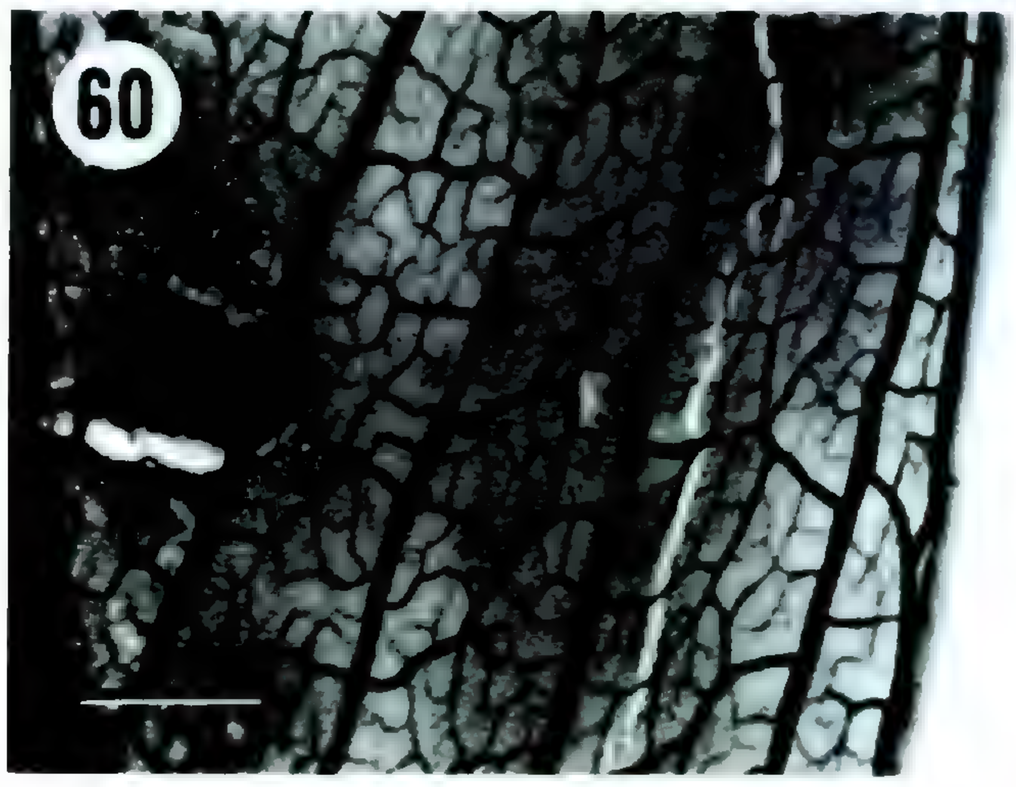
Sect. *Ghaesembilla* Pax & K. Hoffm.

A. ghaesembilla Gaertn., China: Hainan, *Tsang 15564* (UC), Sumatra: *Toroes 4828* (UC).

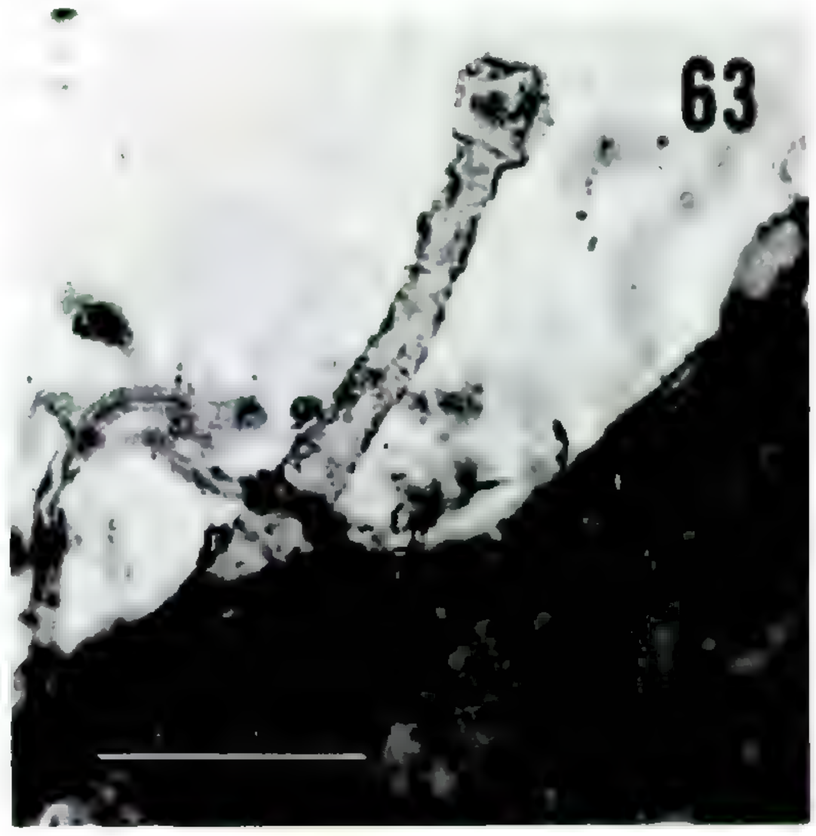
Leaves microphylls to mesophylls, symmetrical, elliptic, narrow elliptic, or narrow obovate; apex typically acuminate or acute, less typically obtuse or rounded; base acute, obtuse, or rounded; organization of venation low to mid third







FIGURES 55–60. Leaves of *Antidesma* and *Celianella*.—55. *Antidesma venosum*.—56. *A. fructifera*.—57. Abaxial epidermis of *A. delicatulum*, showing unicellular trichome.—58. Adaxial epidermis of *A. delicatulum*, showing tanniniferous epidermal cell (arrow).—59, 60. *Celianella montana*. Bars equal 1 cm in Figures 55, 59; 1 mm in Figures 56, 60; 100 μm in Figure 57; and 50 μm in Figure 58.



FIGURES 61–63. Leaves of *Hyeronima* and *Leptonema*.—61. Peltate trichomes of *Hyeronima alchorneoides*.—62. *Leptonema venosa*.—63. Multicellular trichome on margin of leaf of *L. venosa*. Bars equal 5 mm in Figure 62 and 100 μm in Figures 61, 63.

rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes typically present at least beneath low order veins and in many species also scattered on abaxial intercostal areas, less typically over low order veins or the leaves glabrous.

My anatomical observations agree with Rothdauscher (1896) and Gaucher (1902) except in one respect: they reported that stomata were restricted to the abaxial epidermis in all 11 species they examined, including *A. ghaesembilla*. In the two specimens of this species that I examined, I found a few (stomatal index 1–2%) stomata in the adaxial epidermis.

Celianella Jabl. (OTU 35)

C. montana Jabl., Venezuela: Amazonas, *Maguire & Maguire 35071* (US). Figures 59, 60.

Leaves microphylls, symmetrical, oblanceolate; apex acute with a small apiculum; base acute-decurrent; organization of venation low third rank; secondary veins quite numerous and closely spaced, alternating with intersecondaries; tertiary veins percurrent but sinuous; marginal ultimate venation formed by basal secondaries in lower portion of leaf, looped above; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic.

Hyeronima Fr. Allem. (OTU 36)

H. alchorneoides Fr. Allem., Venezuela: Amazonas, *Krukoff 5032* (UC). Figure 61.

H. guatemalensis D. Sm., Costa Rica: *Stork 4213* (UC).

H. poasana Standl., Costa Rica: *Smith 2012* (UC).

Leaves microphylls to mesophylls, symmetrical, elliptic or obovate; apex acuminate; base acute or rounded; organization of venation low to mid third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins lightly sclerified; stomata paracytic; unicellular trichomes beneath primary and secondaries; peltate trichomes scattered on adaxial epidermis, densely covering abaxial epidermis.

My anatomical observations agree with those of Rothdauscher (1896).

Leptonema A. Juss. (OTU 37)

L. venosum (Poir.) Juss., Madagascar: *Decary 13624* (P). Figures 62, 63.

Leaves nanophylls to microphylls, symmetrical, wide elliptic; apex obtuse and cuspidate; base rounded; organization of venation third rank; marginal ultimate venation looped; terminal tracheids swollen; bundle sheath of higher order veins parenchymatous; stomata paracytic; unicellular trichomes scattered on adaxial epidermis, especially beneath low order veins; multicellular, uniseriate trichomes with single-celled glandular heads scattered beneath lower order veins and dense on margins of blade.

Thecacoris A. Juss. (OTU 38)

T. gymnogyne Pax, Cameroons: *Zenker 23* (CAS).

T. leptobotrya (Muell. Arg.) Brennan, Cameroons: *Olorunfemi 30638* (DAV).
T. trichogyne Muell. Arg., Rhodesia: *Brenan & Greenway 8031* (EAH).

Leaves microphylls to mesophylls, symmetrical, obovate or elliptic; apex acute to acuminate; base acute; organization of venation low third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic or occasionally parallelocytic; trichomes dense beneath low order veins and scattered on adaxial epidermis.

The central genera of the Antidesmeae, *Antidesma, Hyeronima,* and *Thecacoris,* have extremely similar leaves, which can be recognized architecturally by their regularly spaced secondaries enclosing more or less parallel-sided intercostal areas and very weakly percurrent tertiaries. The additional combination of paracytic stomata and tanniniferous epidermal cells confirms the identification of members of this tribe. Airy Shaw's (1973) resurrection of the family Stilaginaceae for *Antidesma* receives no support from foliar morphology; his suggestion of a relationship to the Icacinaceae directly contradicts the evidence, for the latter have anomocytic or anisocytic stomata (Metcalfe & Chalk, 1950), fewer, more curving secondaries, more strongly percurrent tertiaries, and generally more orthogonal and organized higher order venation (pers. observ.). In fact, the leaves of some sections of *Antidesma* and *Hyeronima* are so similar that if it were not for the peltate trichomes of *Hyeronima,* one could not reliably distinguish leaves of the two genera.

The other two genera that I examined, *Celianella* and *Leptonema,* have leaves that depart considerably from the typical architecture of the tribe. Both, however, share the tanniniferous epidermal cells and paracytic stomata characteristic of the Antidesmeae, suggesting that they do, in fact, belong here. Pollen evidence supports this placement of *Leptonema* (Köhler, 1965). The alternative treatment, followed by most authors, places *Leptonema* among the genera included in Webster's Phyllantheae. Only the uniseriate, multicellular trichomes with unmodified bases argue strongly for this relationship. However the spherical glandular cell at the apex contrasts markedly with the blunt or tapering, non-glandular terminal cell in the Phyllantheae (cf. Figs. 63, 100, 102). Both phenetic and cladistic analyses of leaf characters place *Leptonema* with the Antidesmeae (Levin, 1986 and in press).

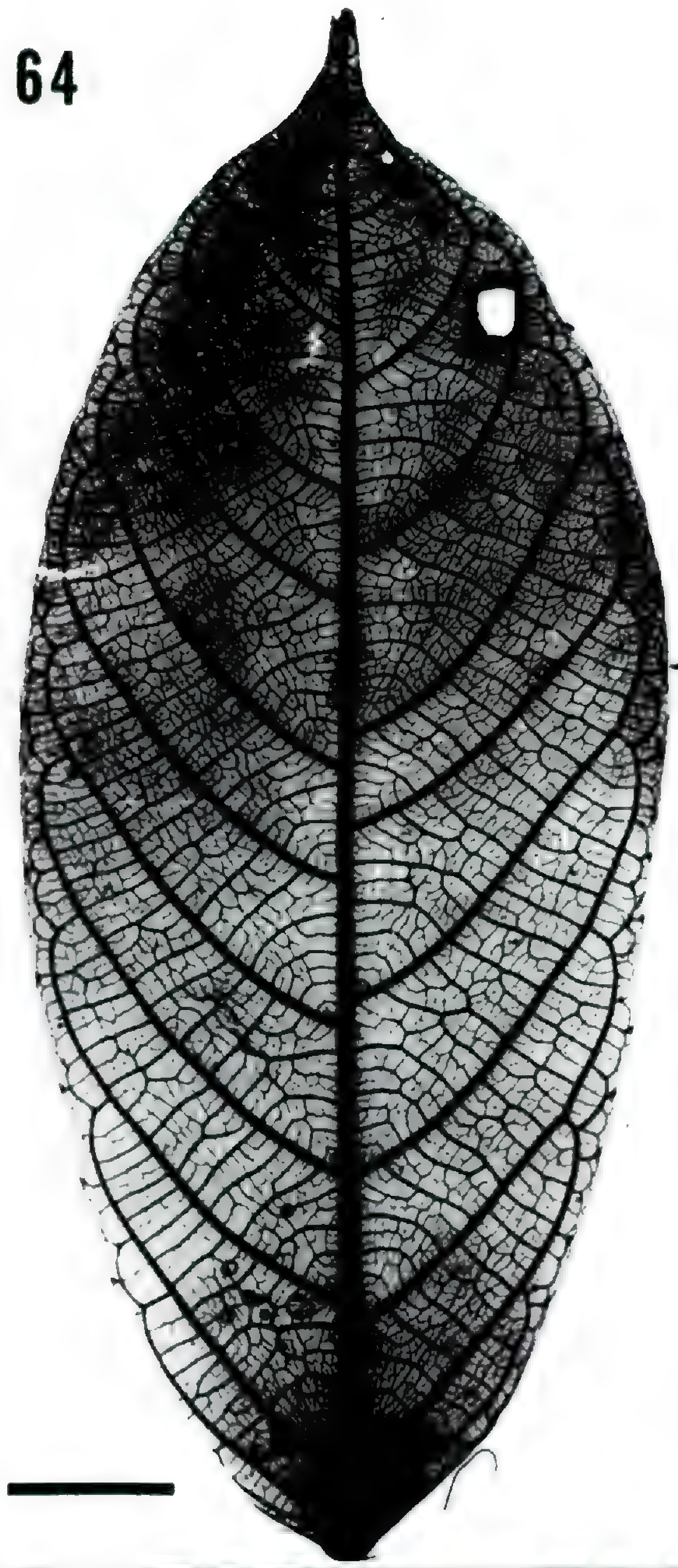
Celianella, described by Jablonsky in 1965, remains poorly known, and its wood and pollen have never been described. Even more so than *Leptonema,* its leaves contrast with the other members of the Antidesmeae. No other phyllanthoids exhibit similar architecture, with numerous, closely spaced secondaries typically alternating with intersecondaries, sinuous, percurrent tertiaries, and few vein orders. However, these features may result from modification of the basic Antidesmeae-type leaf during evolution of the coriaceous, sub-succulent leaves of this genus, a possibility supported by cladistic analysis (Levin, in press).

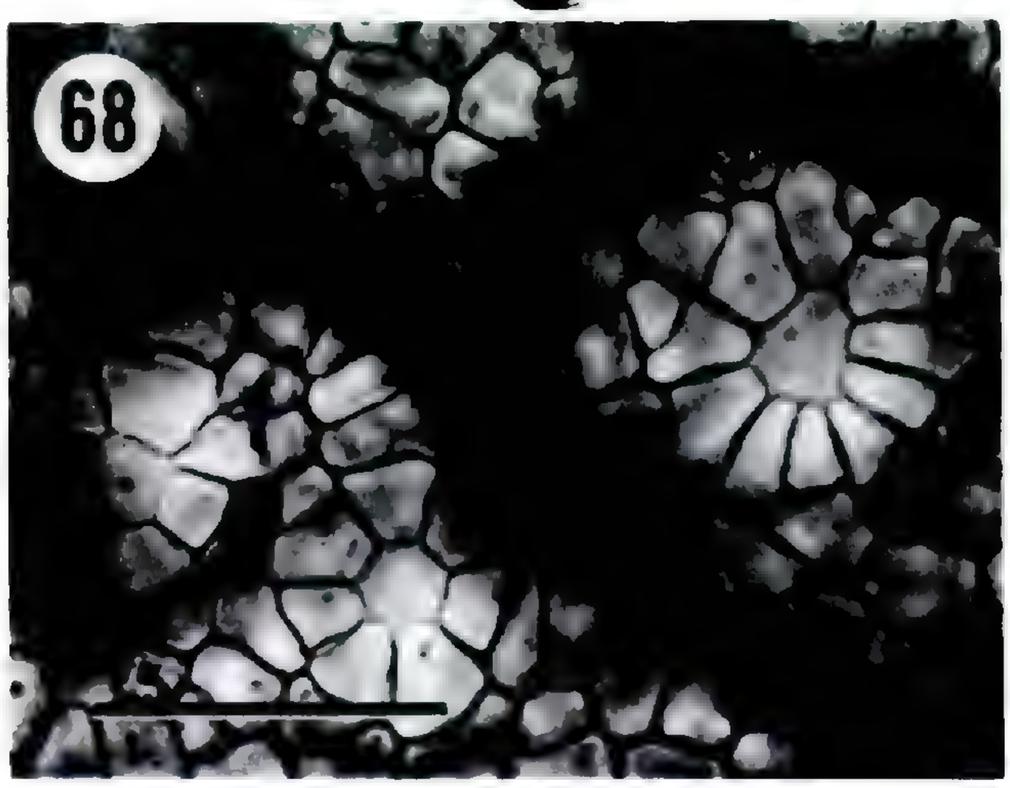
APORUSEAE (LINDL. EX MIQ.) AIRY SHAW

Aporusa Bl. (OTU 39)
A. aurita (Tul.) Miq., Philippines: *Salvoza (1924)* (UC). Figure 67.
A. chinensis (Champ.) Merr., China: Hainan, *Gressitt 876* (UC).
A. frutescens Blume, British N Borneo: *Ramos 1364* (UC). Figures 64, 65.
A. lanceolata Hance, China: Kwangtung, *Chun 6391* (UC). Figure 66.
A. microcalyx Hassk., Indonesia, *cult. Hort. Bog.* (UC 234706).
A. sphaeridophora Merr., Philippines: *Cenabre (1924)* (UC).
A. symplocifolia Merr., Philippines: *Loher 14360* (UC). Figure 68.
A. villosa (Lindl.) Baill., Siam: *Rock 1673* (UC).

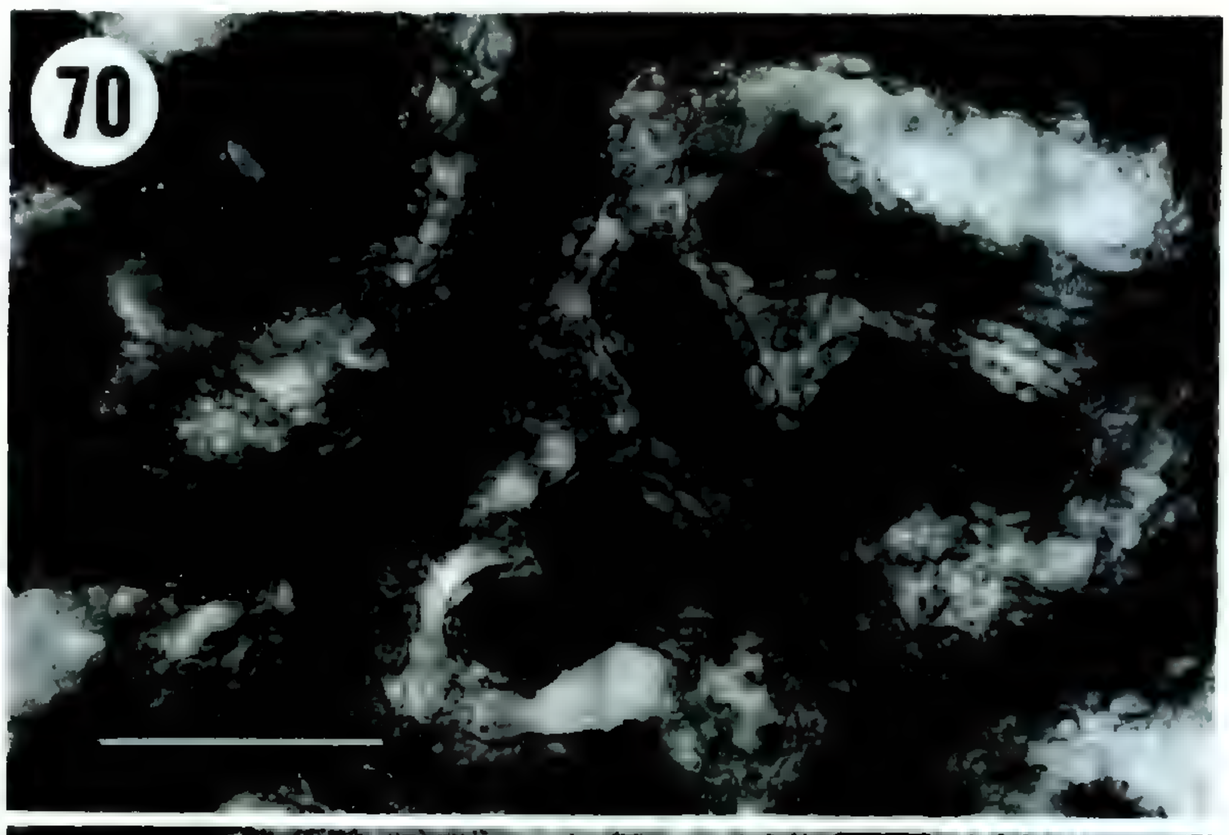
Leaves microphylls to mesophylls, symmetrical, lanceolate, ovate, or elliptic; apex acuminate to caudate or obtuse; base acute, obtuse, or rounded; organization of venation low to mid third rank; marginal ultimate venation looped or partially incomplete; terminal tracheids normal or rarely (*A. sphaeridophora*) swollen; bundle sheath of higher order veins parenchymatous; stomata anisocytic; trichomes typically present at least beneath midrib and secondaries, may also be scattered on abaxial epidermis and over midrib and secondaries.

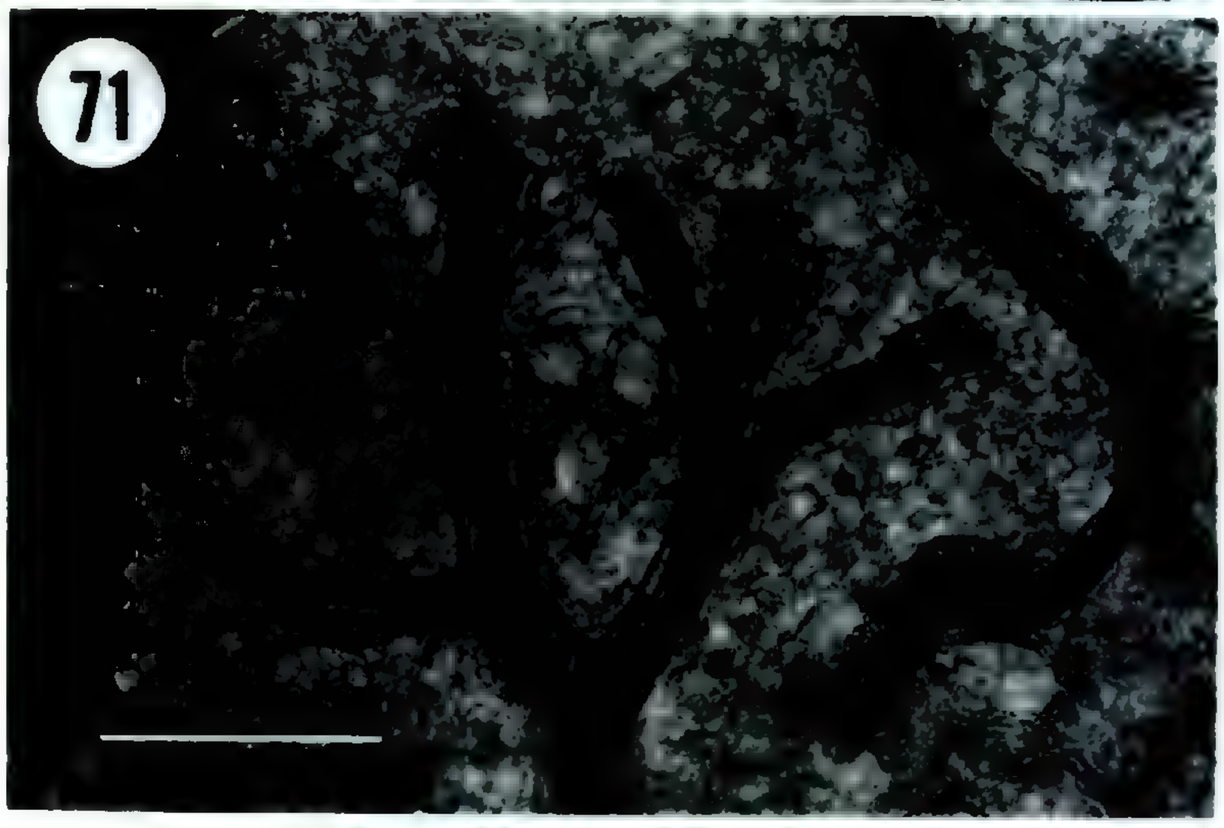
My anatomical observations generally agree with those of Rothdauscher (1896) and Gaucher (1902); as Rothdauscher remarked, the tanniniferous cells in the adaxial epidermis are remarkably large in *Aporusa* and the other genera in the Aporuseae.

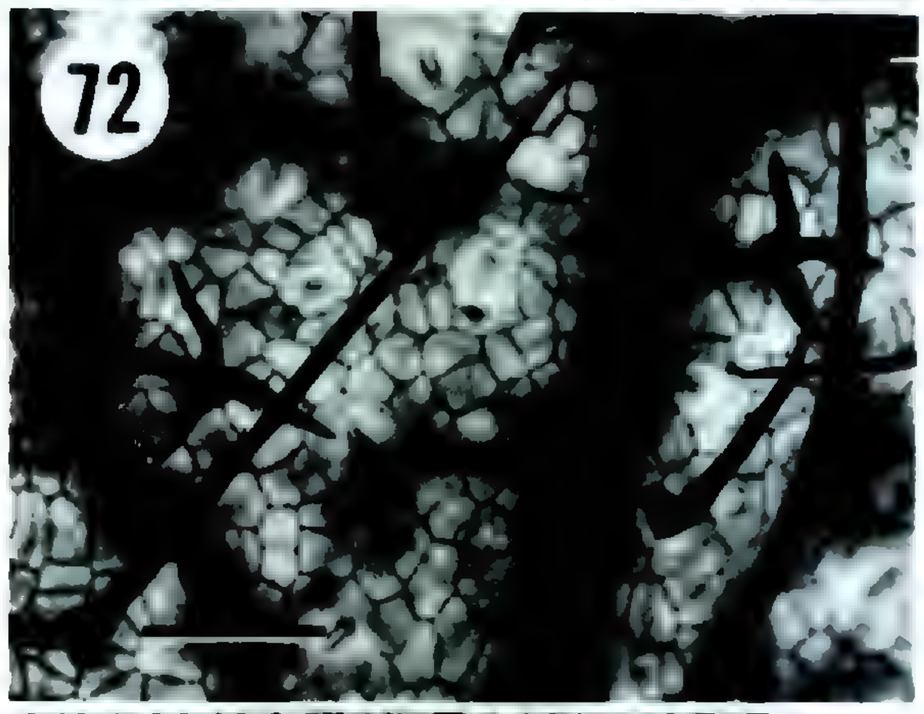


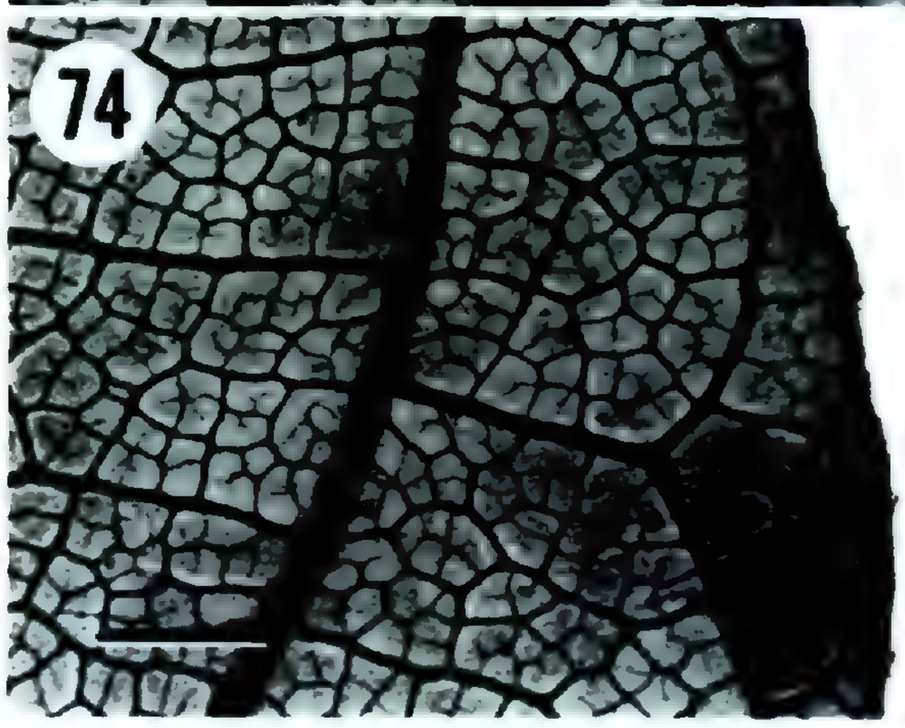


FIGURES 64–68. Leaves of *Aporusa*.—64, 65. *A. frutescens*. Arrow indicates marginal gland.—66. Marginal gland of *A. lanceolata*.—67. Marginal gland of *A. aurita*.—68. Adaxial epidermis of *A. symplocifolia*, with tanniniferous epidermal cells. Bars equal 2 cm in Figure 64; 1 mm in Figure 65; 200 μm in Figures 66, 67; and 100 μm in Figure 68.









FIGURES 69–74. Leaves of *Ashtonia, Baccaurea,* and *Didymocistus.*—69, 70. *Ashtonia praeterita.*—71. *A. whitmorei.*—72. Abaxial epidermis of *Baccaurea deflexa,* with solitary and tufted trichomes.—73, 74. *Didymocistus chrysadenius.* Bars equal 2 cm in Figure 73; 1 cm in Figure 69; 1 mm in Figure 74; 200 μm in Figures 70, 71; and 100 μm in Figure 72.

Ashtonia Airy Shaw (OTU 40)

A. praeterita Airy Shaw, Malaya: *Everett KEP 104934* (A). Figures 69, 70.

A. whitmorei Airy Shaw, Malaya: *Stone 8654* (A). Figure 71.

Leaves microphylls, symmetrical, elliptic; apex obtuse; base obtuse; organization of venation mid third rank; marginal ultimate venation mostly incomplete; terminal tracheids more or less normal (*A. whitmorei*) or swollen (*A. praeterita*); bundle sheath of higher order veins lightly (*A. whitmorei*) or heavily (*A. praeterita*) sclerified; stomata anisocytic; trichomes scattered beneath midrib.

If the specimens I examined are representative, the degree of enlargement of the terminal tracheids and of the sclerification of the bundle sheath allow one to distinguish easily between leaves of the two species (Figs. 70, 71).

Baccaurea Lour.

Group 1 (OTU 41)

Sect. *Calyptroon* (Miq.) Muell. Arg.

B. wilkesiana Muell. Arg., Fiji: *Smith 9692* (UC).

Sect. *Everettiodendron* (Merr.) Pax & K. Hoffm.

B. bracteata Muell. Arg., Singapore: *Ridley 1893* (UC).

B. deflexa Muell. Arg., British N Borneo: *Elmer 21118* (UC). Figure 72.

B. philippinensis Merr., Philippines: *Wenzel 3007* (UC).

Group 2 (OTU 42)

Sect. *Pierardia* (Roxb.) Muell. Arg.

B. obtusa A. C. Smith, Fiji: *Smith 1780* (UC), *Webster & Hildreth 14140* (DAV).

B. pendula Merr., British N Borneo: *Elmer 21290* (UC).

B. racemosa (Reinw.) Muell. Arg., British N Borneo: *Elmer 21195* (UC).

Group 3 (*Dubiae*) (OTU 43)

B. cauliflora Lour., China: Hainan, *Fung 20024* (UC).

Group 4 (OTU 44)

Sect. *Isoandrion* (Baill.) Muell. Arg.

B. stylaris Muell. Arg., Fiji: *Smith 8060* (UC), *Webster & Hildreth 14046* (DAV).

Leaves microphylls to mesophylls, symmetrical, ovate, elliptic, or obovate; apex acuminate, acute, or obtuse; base acute-decurrent, acute, obtuse, or rounded; organization of venation third rank; marginal ultimate venation looped or partially incomplete; terminal tracheids normal; bundle sheath of higher order veins lightly or heavily sclerified; stomata anisocytic, rarely the smallest cell divided again parallel to the guard cells; trichomes typically of two lengths, the longer solitary, the shorter solitary or tufted in groups of 2–5(–8), both scattered beneath lower order veins or generally on abaxial epidermis (Fig. 72), or rarely the leaves glabrous.

Rothdauscher's (1896) and Gaucher's (1902) anatomical observations agree with mine.

Didymocistus Kuhlm. (OTU 45)

D. chrysadenius Kuhlm., Peru: *Asplund 14760* (CAS). Figures 73, 74.

Leaves mesophylls, symmetrical, ovate-elliptic; apex acuminate; base rounded; organization of venation fourth rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic; trichomes of two types, the longer ones solitary, scattered beneath midrib and dense abaxially in junction of midrib and secondaries, the shorter ones tufted in groups of 3–15, scattered on both surfaces but denser abaxially and beneath veins; lower epidermis densely covered with sessile, disk-shaped glands.

Maesobotrya Benth. (OTU 46)

M. barteri (Baill.) Hutch., Liberia: *Leeuwenberg 4851* (MO).

M. bipindensis (Pax) Hutch., Cameroons: *Zenker 2598* (MO).

M. dusenii (Pax) Hutch., Cameroons: *Zenker (1906)* (CAS), *Olorunfemi s.n.* (DAV 47305).

M. floribunda Benth., Congo: *Leonard 251* (UC).

M. pynaertii (De Wild.) Pax & Hoffm., Congo: *Leonard 334* (MO).

M. staudtii (Pax) Hutch., Congo: *Donie 2113* (MO), Cameroons: *Zenker 568* (UC).

Leaves microphylls to mesophylls, symmetrical, elliptic or oblong; apex long acuminate; base acute or obtuse; organization of venation mid third rank; marginal ultimate venation incomplete or partially looped; terminal tracheids normal or somewhat swollen (*M. dusenii* and *M. floribunda*); bundle sheath of higher order veins parenchymatous; stomata anisocytic; trichomes scattered or dense beneath midrib and secondaries and on margin, may also be scattered on abaxial epidermis.

Among the Aporuseae, *Maesobotrya* comes the closest to being toothed, with species such as *M.*

floribunda and *M. staudtii* having denticulate margins.

Protomegabaria Hutch. (OTU 47)
P. stapfiana Hutch., Ghana: *Enti FHI 8167* (G).

Leaves mesophylls, symmetrical, elliptic; apex acute; base acute; organization of venation mid third rank; marginal ultimate venation looped to partially incomplete; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata anisocytic; trichomes dense beneath midrib and secondaries.

Richeria Vahl. (OTU 48)
R. australis Muell. Arg., Santa Catarina: *Reitz & Klein 4044* (UC).
R. grandis Vahl., Venezuela: *Wurdack & Monachino 41152* (UC).
R. obovata (Muell. Arg.) Pax & Hoffm., Matto Grosso: *Irwin & Soderstrom 6445* (NY).
R. racemosa (Poepp. & Endl.) Pax & Hoffm., Venezuela: *Maquire & Politi 28440* (DAV).

Leaves mesophylls, symmetrical, obovate; apex acute or obtuse; base acute or obtuse; organization of venation mid third rank; marginal ultimate venation looped to partially incomplete; terminal tracheids normal or swollen; bundle sheath of higher order veins parenchymatous; stomata basically anisocytic, but with a tendency toward being helicocytic; trichomes scattered or dense beneath midrib and proximal portions of secondaries, or the leaves glabrous.

My observations generally agree with those of Rothdauscher (1896), Gaucher (1902), and Hayden (1980), except that Hayden considered the stomata to be anomocytic. Indeed, as Rothdauscher noted, the number of subsidiary cells surrounding each pair of guard cells varies between three and four; this variation, with the concomitant variation in cell size and shape, may suggest the anomocytic pattern. I, however, interpret the stomatal complex as developing in a spiral pattern, described by Payne (1970) as giving rise to either anisocytic or helicocytic stomata.

The Aporuseae were first recognized as a distinct group by Köhler (1965), who considered the group closely related to the Antidesmeae, in which the genera had been scattered by earlier authors. Foliar morphology certainly supports this treatment. The architecture of the two tribes is quite similar, but the Aporuseae can be separated on the basis of having much larger tanniniferous cells in the epidermis, anisocytic rather than paracytic stomata, and marginal glands. Also the level of venational organization tends to be higher in the Aporuseae. Cladistic analysis of the leaf characters suggests that the Aporuseae are specialized derivatives of the Antidesmeae (Levin, in press).

The marginal glands, located either on the ends of small teeth or in the sinuses of small crenulations, may represent remnants of the theoid teeth found in *Bischofia, Drypetes,* and *Putranjiva.* However, as the Aporuseae appear not to be particularly closely related to these genera but to be derived from entire-leaved ancestors, the alternative hypothesis that the glands have evolved *de novo* may be more parsimonious (Levin, in press).

Two genera placed in the Aporuseae by Webster (1975) do not conform completely with the typical foliar morphology of the tribe. Of these, *Protomegabaria* departs only in lacking marginal glands. Köhler (1965) commented that pollen characters placed *P. stapfiana* in the Aporuseae, but *P. macrophylla* resembled the Antidesmeae. Perhaps *Protomegabaria* represents an intermediate between these tribes. Alternatively, the glands may be secondarily absent; some other genera have glandless species (e.g., *Richeria obovata*). It would be worthwhile to examine leaves of *P. macrophylla* to determine the stomatal type and size of the tanniniferous epidermal cells.

In contrast, leaves of *Didymocistus* bear little resemblance to the other Aporuseae. In particular, the leaves of *Didymocistus* have more highly organized venation (fourth rank), have brachyparacytic stomata, and lack tanniniferous cells and marginal glands. The high rank and sessile, flat-topped glands suggest a possible relationship with *Hymenocardia.* Certainly the relationships of this little known, monotypic genus deserve far more consideration than Kuhlmann (1940) gave in his original description.

DRYPETEAE (GRISEB.) HURUSAWA

Drypetes Vahl. (Figs. 75–82)
See Table 4 for species examined.

Leaves microphylls to mesophylls, symmetrical, ovate, elliptic, oblong, or obovate; apex attenuate, acuminate, acute, or obtuse; base broadly acute, obtuse, or rounded, almost invariably oblique; organization of venation mid second to mid third rank; marginal ultimate ve-

TABLE 4. Species of *Drypetes* examined.

Species	Collector	Location	Herbarium
Group 1 (OTU 49)			
Sect. *Drypetes*			
alba Poit.	*Ekman 12160*	Hispanolia	DAV
diversifolia Krug & Urban	*Hackett 188*	Bahamas	UC
Sect. *Sphragidia* (Thwait.) Pax & Hoffm.			
aframensis Hutch.	*Mensah FH 6732*	Ghana	GC
floribunda (Muell. Arg.) Hutch.	*Hall & Enti 40228*	Ghana	GC
natalensis (Harv.) Hutch.	*Wood (1891)*	Natal	MO
rhakodiscos (Hassk.) Airy Shaw	*Elmer 20768*	British N Borneo	UC
principum (Muell. Arg.) Hutch.	*Hall & Abbiw 44753*	Ghana	GC
Sect. unknown			
ivorensis Hutch. & Dalz.	*Hall & Abbiw 43178*	Ghana	GC
lisolinoli Leonard	*Leonard 1186*	Congo	UC
littoralis (C. B. Rob.) Merr.	*Keinholz (1924)*	Philippines	UC
Group 2 (OTU 50)			
Sect. *Drypetes*			
ilicifolia Kr. & Urb.	*Proctor 31554*	Jamaica	DAV
pellegrini Leandri	*Hall & Abbiw 44118*	Ghana	GC
perreticulata Gagnep.	*Lau 304*	China, Hainan	UC
standleyi Webster	*Foster & Croat 2308*	Panama	DAV
Sect. *Sphragidia* (Thwait.) Pax & Hoffm.			
assamicus Pax & Hoffm.	*Soejarto 102*	Indonesia, cult. Hort. Bog.	DAV
aylmeri Hutch. & Dalz.	*Hall & Abbiw 44147*	Ghana	GC
battiscombei Hutch.	*Tanner 1326*	Tanganyika	UC
Sect. unknown			
gosseweileri S. Moore	*Louis 11651*	Congo	UC
iwahigensis Merr.	*Elmer 17290*	Philippines	UC
Group 3 (OTU 51)			
Sect. *Sphragidia* (Thwait.) Pax & Hoffm.			
laevis (Miq.) Pax & Hoffm.	*Soejarto 95*	Indonesia, cult. Hort. Bog.	DAV
maquilingensis Merr.	*unknown*	Philippines	UC 272672
ramiflora Pax & Hoffm.	*Ramos & Edano (1928)*	Philippines	UC
Group 4 (OTU 52)			
Sect. *Oligandrae* Pax & Hoffm.			
gerrardii Hutch.	*Brass 17837*	Nyasaland	UC
lateriflora (Sw.) Kr. & Urb.	*unknown*	Mexico, Sonora	UC 44009
Sect. *Stemonodiscus* Pierre in sched.			
arguta (Muell. Arg.) Hutch.	*Schlieben 3953*	Tanganyika	MO
capillipes Pax & Hoffm.	*Louis 3479*	Congo	UC
chevalieri Beille	*Hall 43837*	Ghana	GC
gilgiana Pax & Hoffm.	*K. Da— (ill.) 215*	Gold Coast	MO
gilgiana Pax & Hoffm.	*Hall & Abbiw 43781*	Ghana	GC
leonensis Pax	*Hall & Abbiw 44732*	Ghana	GC
parvifolia (Muell. Arg.) Pax & Hoffm.	*Hall 1192*	Ghana	GC
staudtii (Pax) Hutch.	*Zenker 3398*	Cameroons	MO
Sect. *Stipulares* Pax & Hoffm.			
singroboensis Ake Assi	*Hall & Swaine 43266*	Ghana	GC

TABLE 4. Continued.

Species	Collector	Location	Herbarium
Group 5 (OTU 53)			
Sect. *Oligandrae* Pax & Hoffm.			
aubrevillei Leandri	*Hall & Swaine 43239*	Ghana	GC
Sect. *Stipulares* Pax & Hoffm.			
bipindensis (Pax) Hutch.	*Zenker 3788*	Cameroons	MO
Group 6 (OTU 54)			
Sect. *Drypetes*			
australasica Muell. Arg.	*Clemens (1944)*	Australia, Queensland	UC
deplanchei Brongn. & Gris	*McKee 1996*	New Caledonia	UC
glauca Vahl	*Webster et al. 8790*	Puerto Rico	DAV
vitiensis Croizat	*Parks 20691*	Fiji	UC

nation typically looped or fimbriate, less typically incomplete; terminal tracheids normal; bundle sheath of higher order veins parenchymatous or rarely sclerified; stomata brachyparacytic, the subsidiary cells typically almost completely covered by the guard cells.

My observations generally agree with those of Rothdauscher (1896), Gaucher (1902), Smith and Ayensu (1964), and Hayden (1980). Smith and Ayensu, however, reported anomocytic stomata from some species. Having examined many of the same species myself, I suspect that Smith and Ayensu missed the subsidiary cells, which in many species are completely sunken beneath the guard cells and therefore difficult to see in clearings.

The teeth of *Drypetes* are traversed by a single vein that terminates below a clear, deciduous seta (Figs. 80–82), and thus are of the theoid tooth type described by Hickey and Wolfe (1975). The teeth are concave to straight along the upper side, convex along the lower side, with an obtuse apex and rounded sinus. The axis of the tooth forms an angle of about 40° to the tangent of the margin. The teeth are typically regularly distributed along the complete margin, or are absent on the apex if this is attenuate or long acuminate. In many species the teeth are little more than seta-tipped crenations (Fig. 77), whereas in a few (e.g., *D. natalense,* juvenile foliage of *D. diversifolia*) the teeth are spinose.

As the description and Table 1 indicate, leaf architecture in *Drypetes* is quite variable. Interestingly, this variation does not seem to follow Pax and Hoffmann's (1922) classification of the genus (see Table 4), which is based primarily on characters of the gynoecium and disk. Careful study of more of the approximately 160 species will be required in order to evaluate the taxonomic significance of the architectural variation.

Neowawraea Rock (OTU 90)

N. phyllanthoides Rock, U.S.A.: Hawaii, *Webster 13889* (DAV). Figures 83–85.

Leaves mesophylls, symmetrical, ovate; apex broadly acute; base rounded to subcordate; organization of venation fourth rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic.

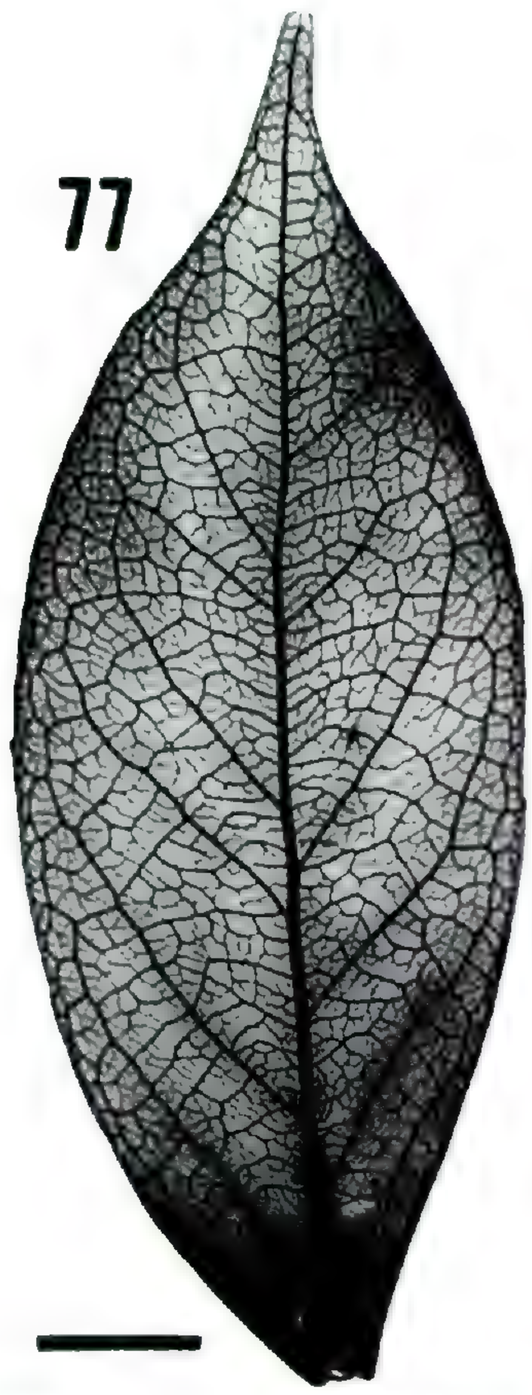
Smith and Ayensu (1964) reported that the stomata were more or less anomocytic and that crystals were absent in the specimen of *N. phyllanthoides* that they examined.

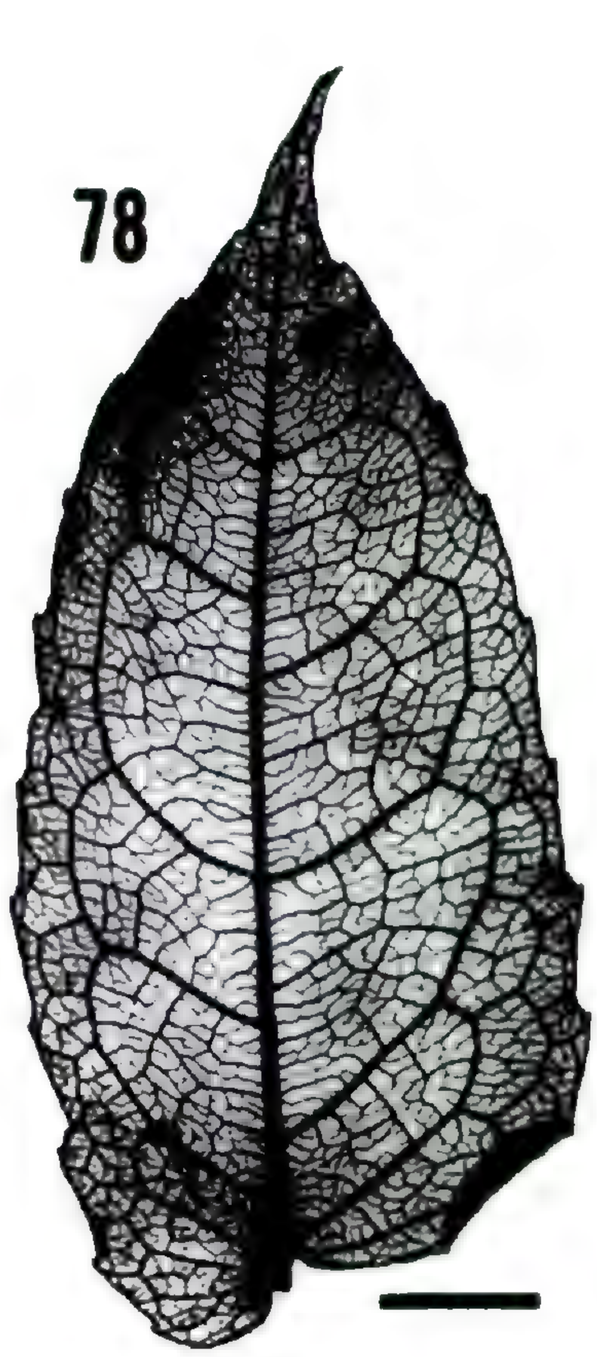
Putranjiva Wall. (OTU 55)

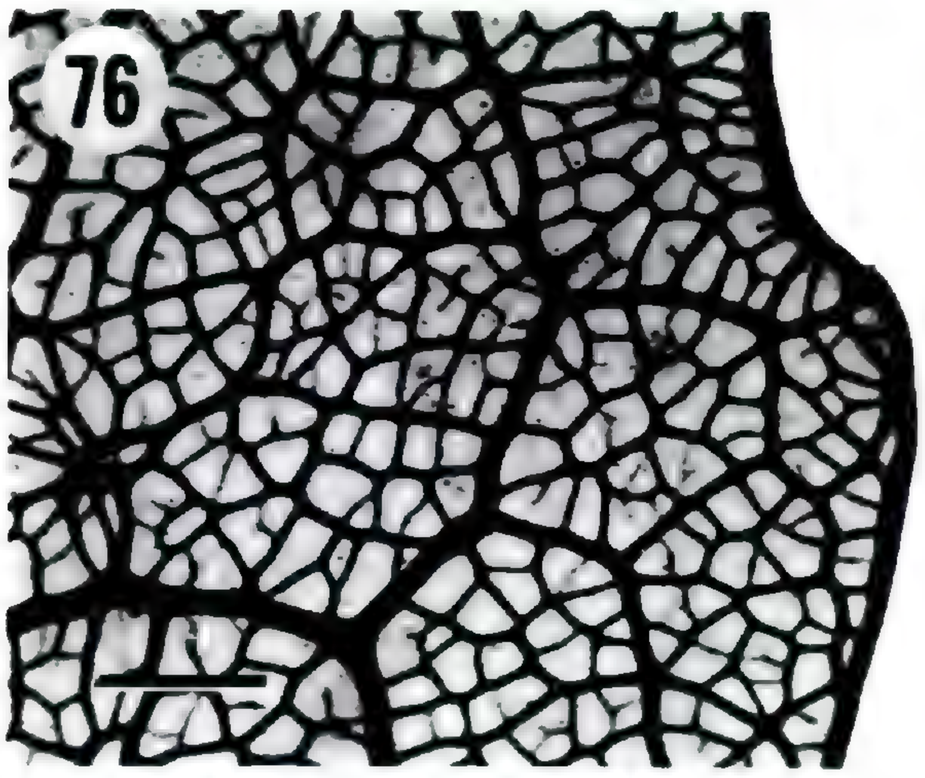
P. roxburghii Wall., Thailand: *collector illeg.* (UC 237213). Figures 86–89.

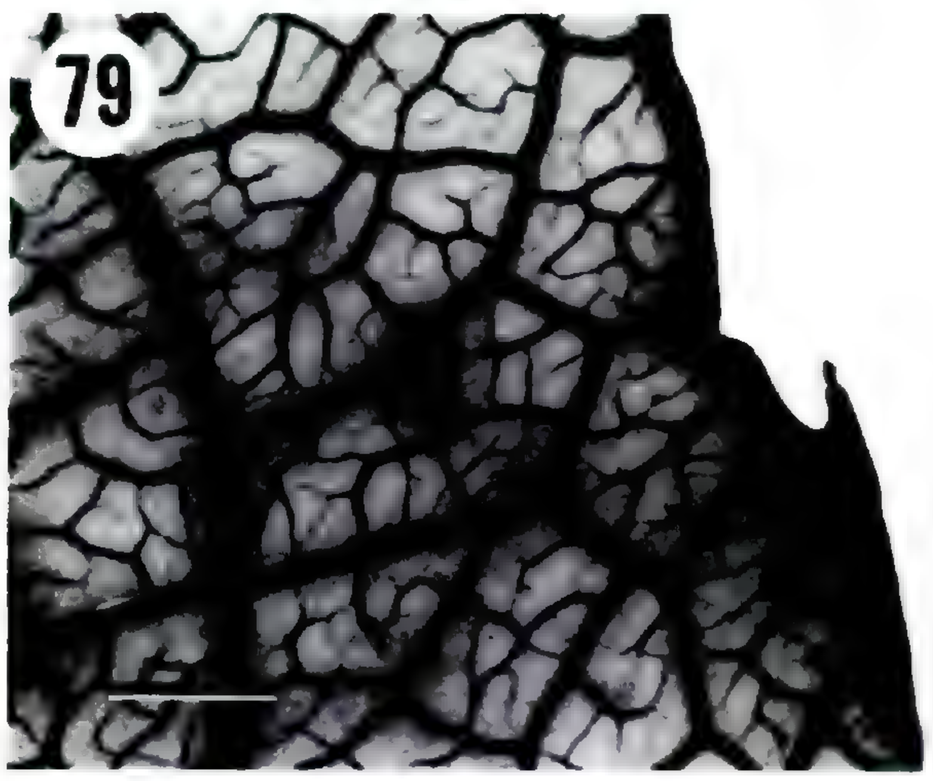
Leaves mesophylls, symmetrical, narrow elliptic; apex acute; base acute; organization of venation high second rank; marginal ultimate venation incomplete; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic.

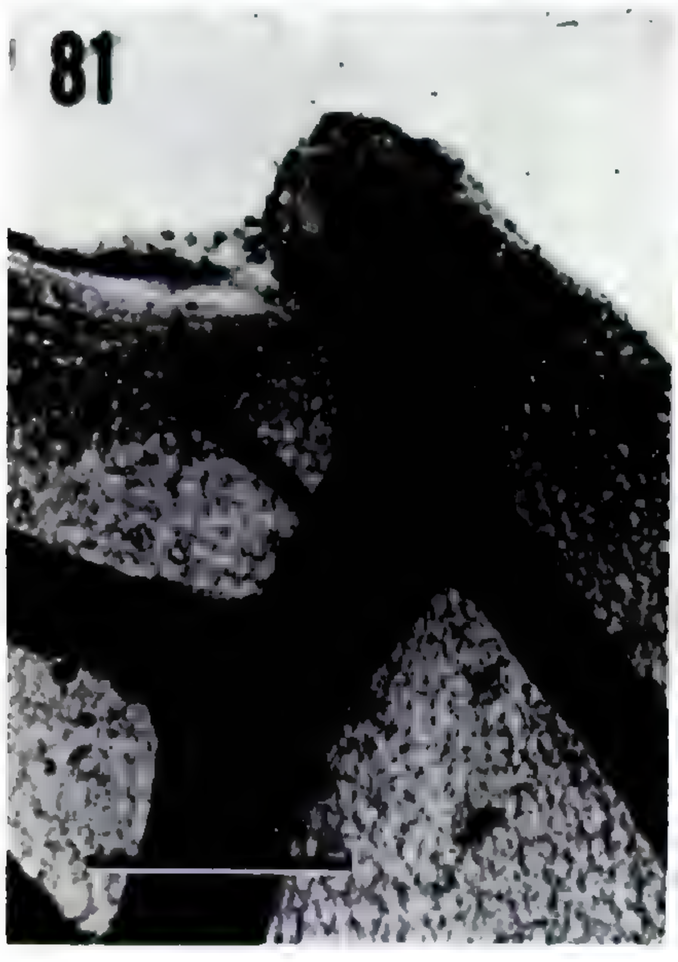
The teeth of *Putranjiva,* like those of *Drypetes,* are of the theoid type. The upper side is concave to straight, the basal side convex, the apex acute, and the sinus rounded. The axis of the tooth forms an angle of about 20–25° to the tangent. The teeth are regularly distributed along the complete margin.



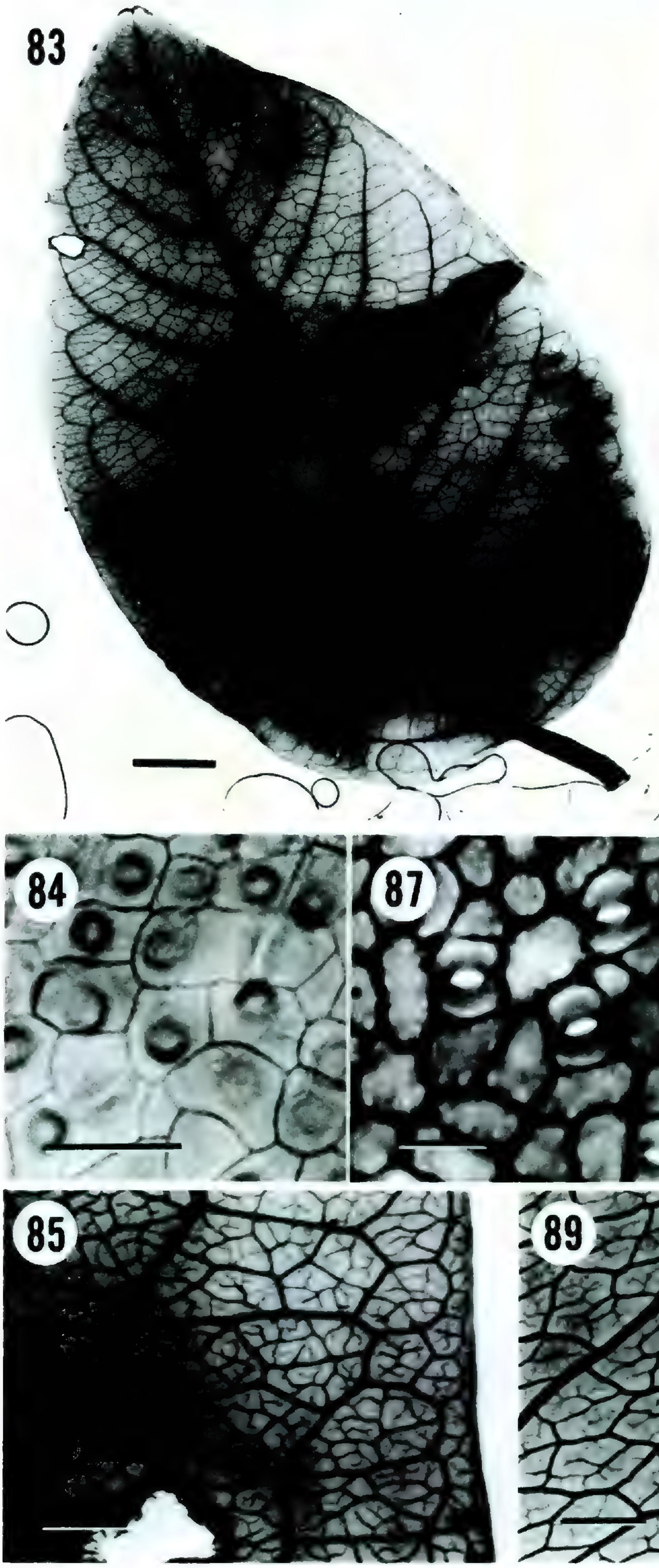


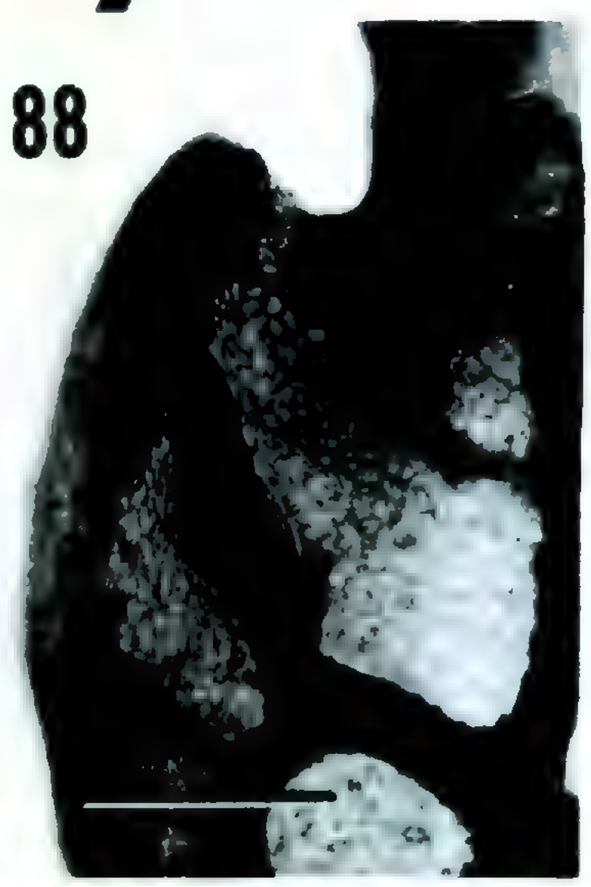


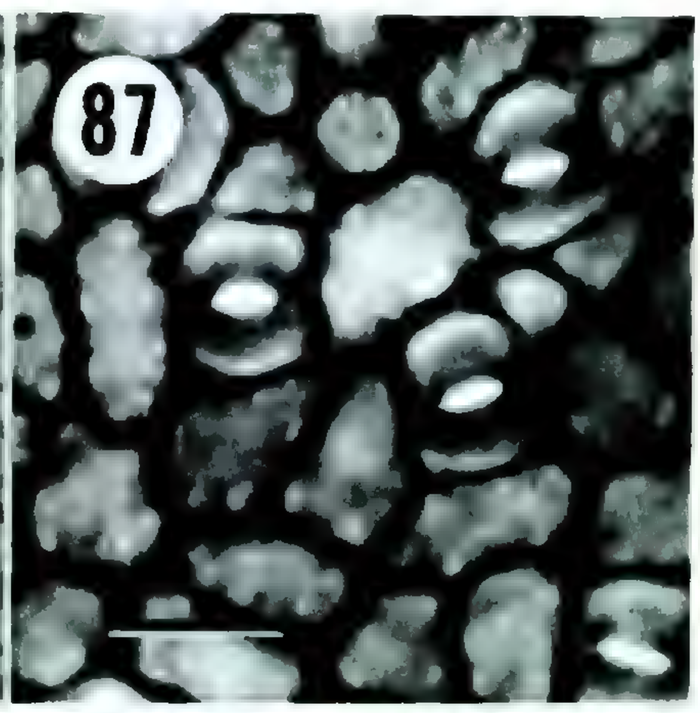


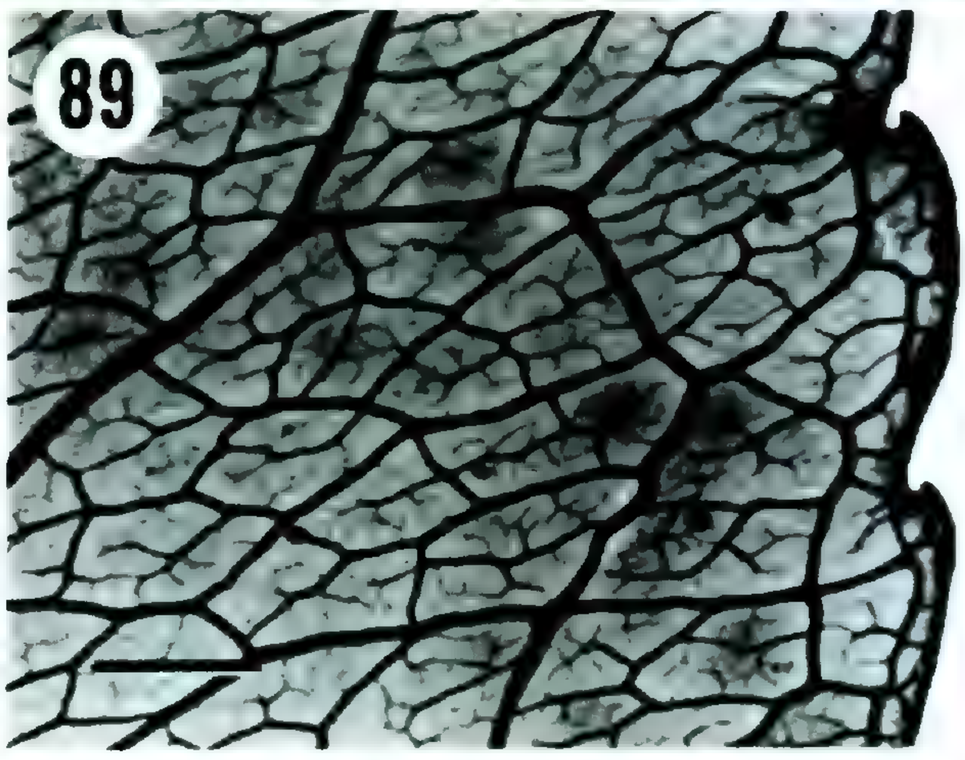


FIGURES 75–82. Leaves of *Drypetes*.—75, 76. *D. australasica*.—77. *D. battiscombei*.—78–80. *D. chevalieri*. The glandular seta abscises at the base of the darkly stained region.—81, 82. Teeth of *D. arguta*, with and without the deciduous seta. Bars equal 1 cm in Figures 75, 77, 78; 1 mm in Figures 76, 79; and 200 μm in Figures 80–82.









FIGURES 83–89. Leaves of *Neowawraea* and *Putranjiva*.—83–85. *Neowawraea phyllanthoides*. Note the papillae and brachyparacytic stomata in the abaxial epidermis.—86–89. *Putranjiva roxburghii*. Figure 87 shows abaxial epidermis. Bars equal 1 cm in Figures 83, 86; 1 mm in Figures 85–89; 200 μm in Figure 88; and 50 μm in Figures 84, 87.

My anatomical observations agree with Gaucher (1902).

Although Pax and Hoffmann (1922) placed *Putranjiva* in the vicinity of *Glochidion* and *Breynia* on the basis of the lack of a disk and ovary rudiment in the flowers, foliar characters support Bentham's (1880) treatment, followed by Webster (1975) and most other recent authors, in which *Putranjiva* is viewed as a close relative of *Drypetes*. Evidence from wood anatomy (Metcalfe & Chalk, 1950) and pollen morphology (Punt, 1962; Köhler, 1965) also points to this relationship. Some taxonomists, e.g., Hurusawa (1954), have even submerged *Putranjiva* in *Drypetes*. The numerous secondaries, frequent intersecondaries, and closely spaced, acute teeth that arise at a very low angle do make the leaves of *Putranjiva* distinctive, but until more is known about the architectural variation within *Drypetes*, the taxonomic significance of these characteristics cannot be determined.

Neowawraea, however, appears quite distant from *Drypetes*. Rock (1913), when he originally described the genus, likened it to *Phyllanthus*. Indeed, the wide angle of origin of the secondaries, the strongly and regularly percurrent tertiaries that form a more or less uniform oblique angle to the midrib, and the brachyparacytic stomata (Fig. 84) suggest a relationship to the more primitive genera in the Flueggeinae, such as *Margaritaria* and *Flueggea*, a relationship proposed by Stone (1967) on the basis of floral morphology. The wood, which is of the *Glochidion*-type (Hayden & Brandt, 1984), and pollen (Selling, 1947) would be more at home in this subtribe than in the Drypeteae. The putative relationship beween *Neowawraea* and *Drypetes* is particularly suspect in that *D. forbesii* Sherff, which Sherff (1939) used as the basis for reducing *Neowawraea* to synonymy with *Drypetes*, was later determined to be a previously described species of *Xylosma* in the Flacourteaceae (Sherff, 1942).

PHYLLANTHEAE DUMORT./SECURINEGINAE MUELL. ARG.

Jablonskia Webst. (OTU 56)
J. congesta (Muell. Arg.) Webst., Venezuela: Amazonas, *Ducke 1631* (UC). Figures 90, 91.

Leaves mesophylls, symmetrical, ovate to lanceolate; apex acute; base acute-cuneate; organization of venation second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic or parallelocytic (with three or more lateral subsidiary cells parallel to the guard cells; Payne, 1970).

My anatomical observations agree with Rothdauscher's (1896) description of this species under its earlier name, *Securinega congesta*.

Keayodendron Leandri (OTU 57)
K. bridelioides (Mildbr.) Leandri, Gold Coast: *Vigne 3122* (A). Figure 95.

Leaves mesophylls, symmetrical, wide-elliptic; apex rounded; base obtuse-decurrent; organization of venation mid to high second rank; marginal ultimate venation fimbriate; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; trichomes scattered beneath midrib and secondaries and on margins.

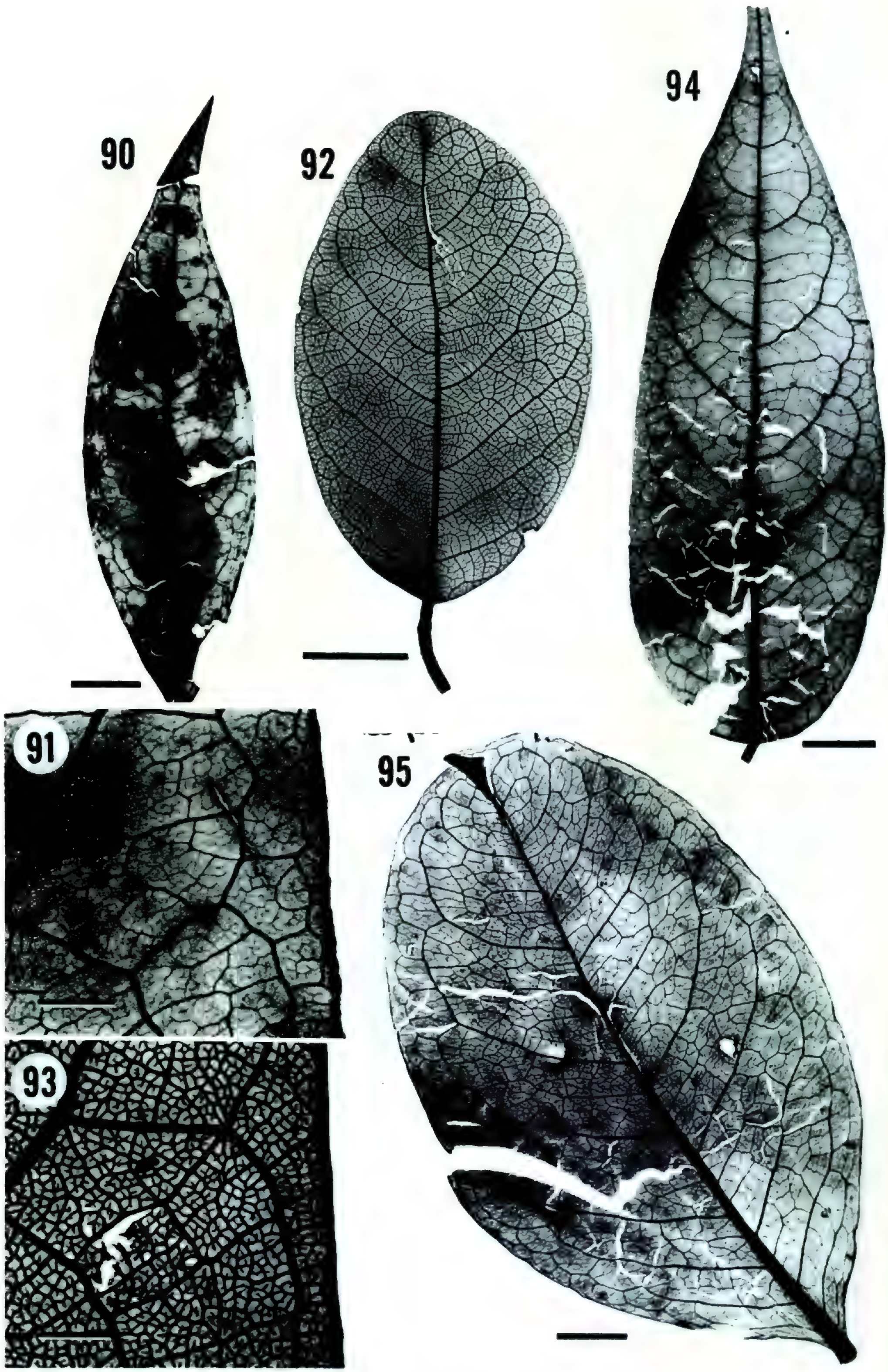
Lingelsheimia Pax (OTU 94)
L. frutescens Pax, Congo: *Leonard 1759* (UC).

Leaves mesophylls, symmetrical, elliptic; apex acuminate; base acute; organization of venation low third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic, rarely the subsidiary cells extending beyond the guard cells at one end (Fig. 96).

Meineckia Baill. (OTU 58)
M. capillipes (Blake) Webst., Guatemala: *Pittier 384* (US).
M. neogranatensis (Muell. Arg.) Webst., Brazil: *Glaziou 13193* (DAV).
M. parvifolia (Wight) Webst., Ceylon: *Wheeler 12227* (DAV).

Leaves nanophylls to microphylls, symmetrical, elliptic or ovate; apex acute or obtuse; base acute, obtuse, or rounded; organization of venation high second to low third rank, the veins very fine; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic.

Raju and Rao (1977) reported that the stomata of *M. parvifolia* are predominantly anisocytic. The specimens of all three species I examined possess paracytic stomata almost exclusively.



FIGURES 90–95. Leaves of Securineginae.—90, 91. *Jablonskia congesta*.—92. *Pseudolachnostylis maprounifolia*.—93. *P. glauca*.—94. *Zimmermannia acuminata*.—95. *Keayodendron bridelioides*. Bars equal 1 cm in Figures 90, 92, 94, 95 and 1 mm in Figures 91, 93.

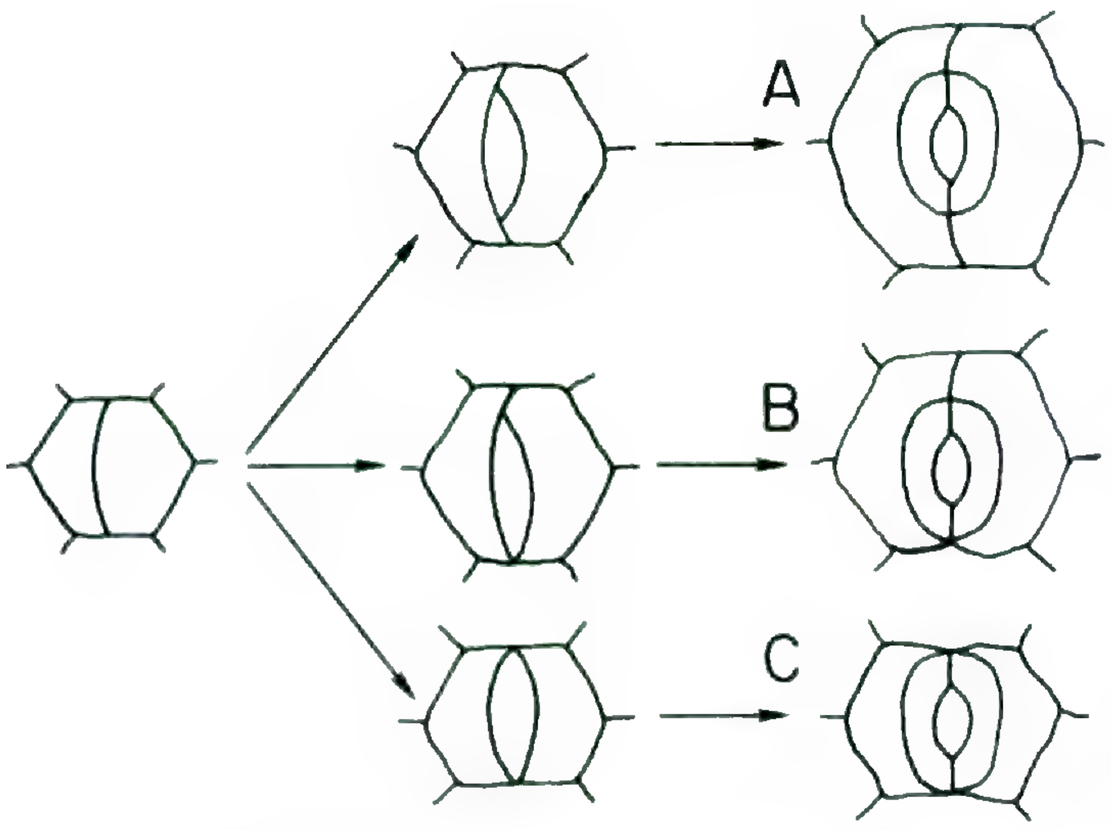


FIGURE 96. Developmental sequence typical of Flueggeinae, giving rise to paracytic (A), intermediate (B), and brachyparacytic (C) stomata. All three types appear on most leaves.

Pseudolachnostylis Pax (OTU 59)

P. dekindtii Pax, Rhodesia: *Coxe 187* (MO).

P. glauca (Hiern) Hutch., Rhodesia: *Rodin 4409* (UC). Figure 93.

P. maprouneifolia Pax, Rhodesia: *Farrell 213* (MO). Figure 92.

P. polygyna Pax & Hoffm., Rhodesia: *Stolz 1754* (CAS).

Leaves microphylls, symmetrical, elliptic or ovate; apex acute or obtuse; base obtuse to rounded or subcordate; organization of venation low fourth rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins sclerified; stomata paracytic; trichomes typically absent, but in *P. dekindtii* dense beneath midrib and secondaries.

My observations agree with those of Gaucher (1902) and Hayden (1980).

Zimmermannia Pax (OTU 60)

Z. acuminata Verdc., Tanganyika: *Vaughn 2665* (EAH). Figure 94.

Z. capillipes Pax, Tanganyika: *Greenway 5862* (MO).

Leaves microphylls to mesophylls, symmetrical, narrow elliptic or lanceolate; apex acute or acuminate; base obtuse to rounded; organization of venation low third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic.

Webster's (1975) Securineginae consist of a collection of genera not found together in any other system. Pollen evidence (Punt, 1962; Köhler, 1965) suggests two groups of genera, one consisting of *Danguyodrypetes*, *Lingelsheimia*, *Pleiostemon*, and *Zimmermannia*, and the other consisting of *Securinega* (except *S. congesta*; see below) and *Chascotheca*. Both Punt and Köhler related *Pseudolachnostylis* to *Amanoa*. The position of *Meineckia* is unclear and *Keayodendron* pollen has not been described.

Leaf morphology does little to clarify the relationships in this group, largely because the genera with aberrant pollen frequently have aberrant leaf morphology. *Lingelsheimia* and *Zimmermannia* have very similar leaves. *Pseudolachnostylis*, with its high rank leaves, is far more specialized than *Amanoa*; there is little to suggest a close relationship between the two genera. Unfortunately, the leaves of *Pseudolachnostylis* are also more specialized than the other Securineginae, although there are trends toward increasing rank in this subtribe, making *Pseudolachnostylis* more at home here than elsewhere. *Meineckia*, in contrast, exhibits lower rank, and appears most similar to *Andrachne*. This could be convergence, as both genera have herbaceous tendencies and small, thin leaves in which reversion to lower rank would be expected. Webster (1965) suggested that *Zimmermannia* is the closest relative of *Meineckia*; the leaves of the latter could easily be derived from the former by reduction in rank associated with the change in habit.

In his review of the pollen of the Euphorbiaceae, Punt (1962) pointed out that the pollen of *Securinega congesta* differed radically from the pollen of other species of *Securinega* he studied. Webster (1984b) described the new genus *Jablonskia* for this species. The leaves suggest a relationship to the Wielandieae, which also have numerous intersecondaries and random to orthogonally reticulate tertiaries. I have not examined leaves of the species that Webster maintained in *Securinega*.

FLUEGGEINAE MUELL. ARG.

Flueggea Willd. (OTU 61)

F. flexuosa Muell. Arg., Philippines: Luzon, *Elmer 15662* (UC).

F. suffruticosa (Pallas) Baillon, Hondo: *Ohwi (1951)* (UC). Figures 97, 98.

F. virosa Roxb. ex Willd., Ivory Coast: *Leeuwenberg 3317* (UC), Tanganyika: *Tanner 4266* (UC).

Leaves microphylls to mesophylls, symmetrical, elliptic; apex acute; base obtuse; organi-

zation of venation mid third rank; marginal ultimate venation incomplete or looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic or with the subsidiary cells extending beyond the guard cells at one end only (Fig. 96).

Gaucher (1902) reported sclerified bundle sheaths in *F. suffruticosa*.

I am following Webster (1984a), who recognized *Flueggea* as a genus distinct from *Securinega*.

Breynia Forst. (OTU 62)

B. acuminata Muell. Arg., Philippines: Luzon, *Clemens 16742* (UC).

B. angustifolia Hook. f., Sumatra: *Boeea 8969* (UC).

B. cernua Muell. Arg., Culion: *Herre 1024* (UC).

B. discigera Muell. Arg., Sumatra: *Yates 1171* (UC). Figure 100.

B. disticha Forst., Tuamotu Island: *Wilder 1148* (UC), Fiji: *Smith 9623* (UC). Figure 99.

B. fruticosa (L.) Hook. f., Hong Kong: *Taam 1771* (UC).

B. officinalis Hemsl., Hong Kong: *Chun 5072* (UC).

Leaves microphylls, symmetrical, ovate, elliptic, or oblong; apex acute, obtuse, or rounded; base acute, obtuse, or rounded, in many species decurrent; organization of venation high third rank; marginal ultimate venation incomplete or partially looped; terminal tracheids normal or swollen (*B. acuminata, B. angustifolia, B. cernua*); bundle sheath of higher order veins parenchymatous; stomata paracytic to brachyparacytic, in many the subsidiary cells extending beyond the guard cells at one end only (Fig. 96); trichomes absent on most species, but *B. discigera* with trichomes covering abaxial epidermis (Fig. 100); epidermal cells typically papillate, in some the papillae quite elongate.

My observations of the species examined by Gaucher (1902), Raju and Rao (1977), and Hayden (1980) agree with their reports.

Glochidion Forst.

See Table 5 for species examined. (Figs. 101, 102)

Leaves microphylls or small mesophylls, symmetrical or asymmetrical (sect. *Hemiglochidion* pro parte), ovate, elliptic, or obovate; apex acuminate, acute, obtuse, or rounded; base acute, obtuse, rounded, or cordate, oblique in species with asymmetrical blades; organization of venation high third rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous or sclerified; stomata brachyparacytic, in some the subsidiary cells extending beyond the guard cells at one end (Fig. 96); trichomes sparse to dense on abaxial epidermis, particularly dense beneath veins, in some species also on adaxial epidermis, or the leaves glabrous.

My anatomical observations do not conflict with those of Gaucher (1902).

Three groups of species can be recognized on the basis of leaf architecture. Section *Glochidion* (OTU 63) has symmetrical leaves with tertiaries that are predominantly perpendicular to the midrib. Section *Hemiglochidion* can be divided into two groups, the first (OTU 64) with symmetrical leaves and tertiaries that vary from oblique to perpendicular to the midrib with the angle decreasing upwards in the leaf, and the second (OTU 65) with asymmetrical leaves with oblique bases and tertiaries that are predominantly perpendicular to the midrib.

Margaritaria L. f. (OTU 67)

M. nobilis L., Panama: *Luteyn & Foster 949* (G). Figures 103, 104.

M. obovata (Baill.) Webst., Tanganyika: *Tanner 3774* (UC).

M. scandens (Wr. ex Griseb.) Webst., Bahamas: Andros, *Brace 4867* (NY).

M. tetracocca (Baill.) Webst., Cuba: *Leon & Clemente 23339* (NY).

Leaves microphylls, symmetrical, obovate or elliptic; apex acute, obtuse, or rounded; base acute, obtuse, or rounded; organization of venation mid third rank; marginal ultimate venation looped or fimbrate; terminal tracheids normal; bundle sheath of higher order veins sclerified; stomata brachyparacytic; trichomes none or scattered beneath veins.

Phyllanthus L.

See Table 6 for species examined.

Leaves nanophylls, microphylls, or mesophylls, symmetrical or some asymmetrical, ovate, elliptic, or obovate; apex acuminate, acute, obtuse, or rounded; base acute, obtuse, rounded, or cordate, some oblique; organization of venation low second to mid third rank; marginal ultimate venation incomplete or looped; terminal tracheids normal or swollen; bundle sheath of higher

FIGURES 97–104. Leaves of Flueggeinae.—97, 98. *Flueggea suffruticosa*.—99. *Breynia disticha*.—100. Multicellular trichomes of *B. discigera*.—101. *Glochidion philippicum*.—102. Multicellular trichomes of *G. eriocarpum*.—103, 104. *Margaritaria nobilis*. Bars equal 1 cm in Figures 97, 99, 101, 103; 1 mm in Figures 98, 104; and 100 μm in Figures 100, 102.

TABLE 5. Species of *Glochidion* examined.

Species	Collector	Location	Herbarium
Group 1 (OTU 63)			
Sect. *Glochidion*			
atalotrichum A. C. Smith	*Smith 8747*	Fiji	UC
cordatum (Muell. Arg.) Seem.	*Smith 9403*	Fiji	UC
dasyphyllum K. Koch	*Merrill 10810*	China, Kwangtung	UC
dasyphyllum K. Koch	*Chun 6405*	China, Kwangtung	UC
eriocarpum Champ.	*Lei 899*	China, Hainan	UC
hirsutum Wight	*Boeea 6700*	Sumatra	UC
hongkongense Muell. Arg.	*Chun 4783*	China, Lantoa Island	UC
lancifolium C. B. Rob.	*Ramos & Edano (1924)*	Philippines	UC
littorale Bl.	*Clemens (1915)*	British N Borneo	UC
Group 2 (OTU 64)			
Sect. *Hemiglochidion* Muell. Arg.			
daltoni Kurcz	*Maire 3865*	China, Yunnan	UC
ferdinandi Muell. Arg.	*White (1926)*	Australia, Queensland	UC
fortunei Hance	*Merrill 11369*	China, Kaingsu	UC
merrillii C. B. Rob.	*Clemens 18750*	Philippines	UC
obovatum Sieb. & Zucc.	*Hiroe 14033*	Japan	UC
rubrum Bl.	*Skukor AS 95*	Malaya	UC
seemannii Muell. Arg.	*Smith 8758*	Fiji	UC
Group 3 (OTU 65)			
album (Blco.) Boerl.	*Ramos & Edano (1927)*	Philippines	UC
benguetense Elm.	*Ramos & Edano (1926)*	Philippines	UC
borneense Boerl.	*Yates 2481*	Sumatra	UC
bracteatum Gill.	*Smith 7366*	Fiji	UC
fagifolium Miq.	*Liang 62257*	China, Hainan	UC
hypoleucum (Miq.) Boerl.	*Cenabre (1924)*	Philippines	UC
lanceolatum Hay	*Chuang & Kao 5541*	Taiwan	UC
leiostylum Kurz.	*Toroes 3834*	Sumatra	UC
philippicum (Cav.) C. B. Rob.	*Ramos (1925)*	Philippines	UC
puberum (D.) Hutch.	*Gressitt 1407*	China, Kwangtung	UC
wrightii Benth.	*Gressitt 1111*	China, Hainan	UC

order veins parenchymatous or sclerified; stomata brachyparacytic or the subsidiary cells extending beyond the guard cells at one end (Fig. 96); trichomes present beneath veins or covering the abaxial epidermis, or none; abaxial epidermis typically papillate, the papillae quite long in many species.

The leaves of most *Phyllanthus* species are borne on determinate plagiotropic branches that mimic compound leaves, a condition termed phyllanthoid branching (Webster, 1956, 1967). As the description and Table 1 indicate, these leaves vary considerably, the diversity within this one huge genus equalling or exceeding the entire subfamily. Many more of the 600–700 species must be examined before any evaluation of the overall taxonomic value of the foliar morphology can be made. Early steps in this direction were made by Webster (1956, 1957, 1958) in his monograph of the West Indian species, but far more remains to be done.

Reverchonia A. Gray
R. arenaria A. Gray, U.S.A.: Texas, *Rowell 11531* (DAV). Figure 105.

Leaves nanophylls, symmetrical, narrow-elliptic to oblanceolate; apex obtuse; base acute; margin entire; organization of venation high first rank; venation pinnate, brochidodromous, all the vein orders beyond the primary very fine; primary vein massive, straight; secondary veins

TABLE 6. Species of *Phyllanthus* examined.

Species	Collector	Location	Herbarium
Sect. *Adenoglochidion* Muell. Arg. (OTU 68)			
aeneus Baill.	*Baumann 6295*	New Caledonia	DAV
aeneus Baill.	*Baumann 6286*	New Caledonia	DAV
Sect. *Anisonema* (A. Juss.) Griseb. (OTU 69)			
microcarpus (Benth.) Muell. Arg.	*Bartlett 14708*	Philippines	UC
reticulatus Poir.	*Tanner 3720*	Tanganyika	UC
Sect. *Aporosella* (Chodat) Webster (OTU 70)			
chacoensis Morong.	*Eyerdam & Beetle 22983*	Argentina	UC
Sect. *Cicca* (L.) Muell. Arg. (OTU 71)			
acidus (L.) Skeels	*Mexia 1005*	Nayarit	UC
acidus (L.) Skeels	*Berngardt (1923)*	Philippines (cult.)	UC
distichus H. & A.	*Webster 1631*	Hawaii	UC
Sect. *Eleutherogynium* Muell. Arg. (OTU 72)			
induratus S. Moore	*Baumann 12504*	New Caledonia	DAV
loranthoides Baill.	*Webster 14780*	New Caledonia	DAV
Sect. *Emblica* (Gartn.) Baill. (OTU 73)			
emblica L.	*Lei 446*	China, Hainan	UC
Sect. *Floribundi* Pax & Hoffm. (OTU 74)			
floribundus Muell. Arg.	*Tanner 3022*	Tanganyika	UC
Subg. *Gomphidium* Baill.			
Group 1 (OTU 75)			
comptonii (S. Moore) Guill.	*Guillaumin 9520*	New Caledonia	US
comptonii (S. Moore) Guill.	*Webster 14829*	New Caledonia	DAV
ripicolus Guill.	*Guillaumin 7232*	New Caledonia	A
Group 2 (OTU 76)			
balanseanus Guill.	*Webster 14735*	New Caledonia	DAV
bourgeosii Baill.	*Guillaumin & Baumann 7547*	New Caledonia	DAV
buxoides Guill.	*McMillan 5103*	New Caledonia	UC
cornutus Baill.	*Baumann 13486*	New Caledonia	DAV
pancherianus Baill.	*Guillaumin & Baumann 6577*	New Caledonia	DAV
poumensis Guill.	*Webster 14642*	New Caledonia	DAV
poumensis Guill.	*McKee 4620*	New Caledonia	UC
Sect. *Hemicicca* (Baill.) Muell. Arg. (OTU 77)			
flexuosus (Sieb. & Zucc.) Muell. Arg.	*Kasapligil 3640*	China, Honshu	UC
Sect. *Heteroglochidion* Muell. Arg. (OTU 78)			
baladensis Baill.	*Webster 14875*	New Caledonia	DAV
francii Guill.	*Guillaumin 8408*	New Caledonia	DAV
peltatus Guill.	*Webster 14645*	New Caledonia	DAV
pronyensis Guill.	*Webster 14414*	New Caledonia	DAV
salacioides S. Moore	*Webster 14871*	New Caledonia	DAV
serpentinus S. Moore	*McKee 4568*	New Caledonia	UC
Sect. *Nothoclema* Webster (OTU 79)			
acuminatus Vahl.	*Dwyer & Duke 7916*	Panama	UC
acuminatus Vahl.	*Hinton et al. 15965*	Mexico	UC

TABLE 6. Continued.

Species	Collector	Location	Herbarium
Sect. *Nymphanthus* (Lour.) Muell. Arg. (OTU 80)			
ruber (Lour.) Spreng.	*Gressitt s.n.*	China, Hainan	UC 1352893
Sect. *Paragomphidium* Muell. Arg. (OTU 81)			
vieillardii Baill.	*Webster 14711*	New Caledonia	DAV
Sect. *Phyllanthodendron* (Hemsl.) Beille (OTU 82)			
mirabilis Muell. Arg.	*Wolfe (1964)*	England, cult. Kew	—
Sect. *Polyandroglochidion* S. Moore (OTU 83)			
ngoyensis Schltr.	*McMillan 5184*	New Caledonia	UC
Sect. *Psychoglochidion* Muell. Arg. (OTU 84)			
koghiensis Guill.	*Webster 14589*	New Caledonia	DAV
Sect. *Scepasma* (Bl.) Muell. Arg. (OTU 85)			
buxifolius (Bl.) Muell. Arg.	*Ramos (1923)*	Philippines	UC

arising acutely at a more or less uniform angle of about 50°, course curved abruptly, loops joining at an obtuse angle; tertiary veins originating at random angles, transverse ramified; highest vein order tertiary; marginal ultimate venation incomplete; areoles extremely irregular in size and shape; veinlets branched once or twice; terminal tracheids swollen; bundle sheath of all veins parenchymatous; epidermal cells isodiametric; arranged randomly, with straight anticlinal walls; stomata equally abundant on both epidermises (stomatal frequency about 12%), with anomocytic stomata; trichomes and crystals absent.

My observations agree with Hayden (1980).

Richeriella Pax & Hoffm. (OTU 86)

R. gracilis (Merr.) Pax & Hoffm., China: Hainan, *Liang 65438* (UC).

Leaves microphylls, symmetrical, elliptic; apex acuminate; base obtuse; organization of venation mid second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic.

Sauropus Bl. (OTU 87)

S. androgynus (L.) Merr., Malaya: *Yapp 198* (UC).

S. grandifolius Pax & Hoffm., Cochinchina: *Pierre s.n.* (UC).

S. hirsutus Beille, Cochinchina: *Pierre 564* (UC).

S. rhamnoides Bl., British N Borneo: *Elmer 20803* (UC).

S. spectabilis Miq., Indonesia: *cult. Hort. Bog.* (UC 301610).

Leaves microphylls to mesophylls, symmetrical, lanceolate, ovate, or elliptic; apex acuminate, acute, or obtuse; base obtuse; organization of venation mid to high third rank; marginal ultimate venation incomplete; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata brachyparacytic to paracytic, the subsidiary cells extending beyond the guard cells at one end only (Fig. 96).

My anatomical observations on these five species agree with Rothdauscher (1896), who studied four others.

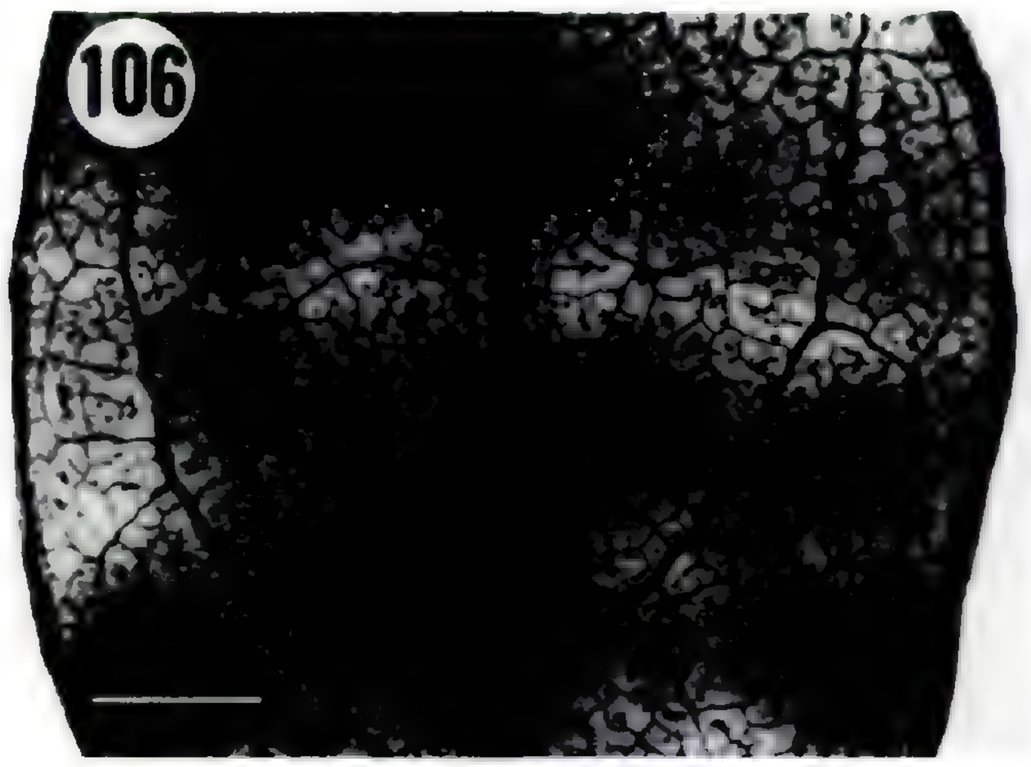
Synostemon F. Muell. (OTU 66)

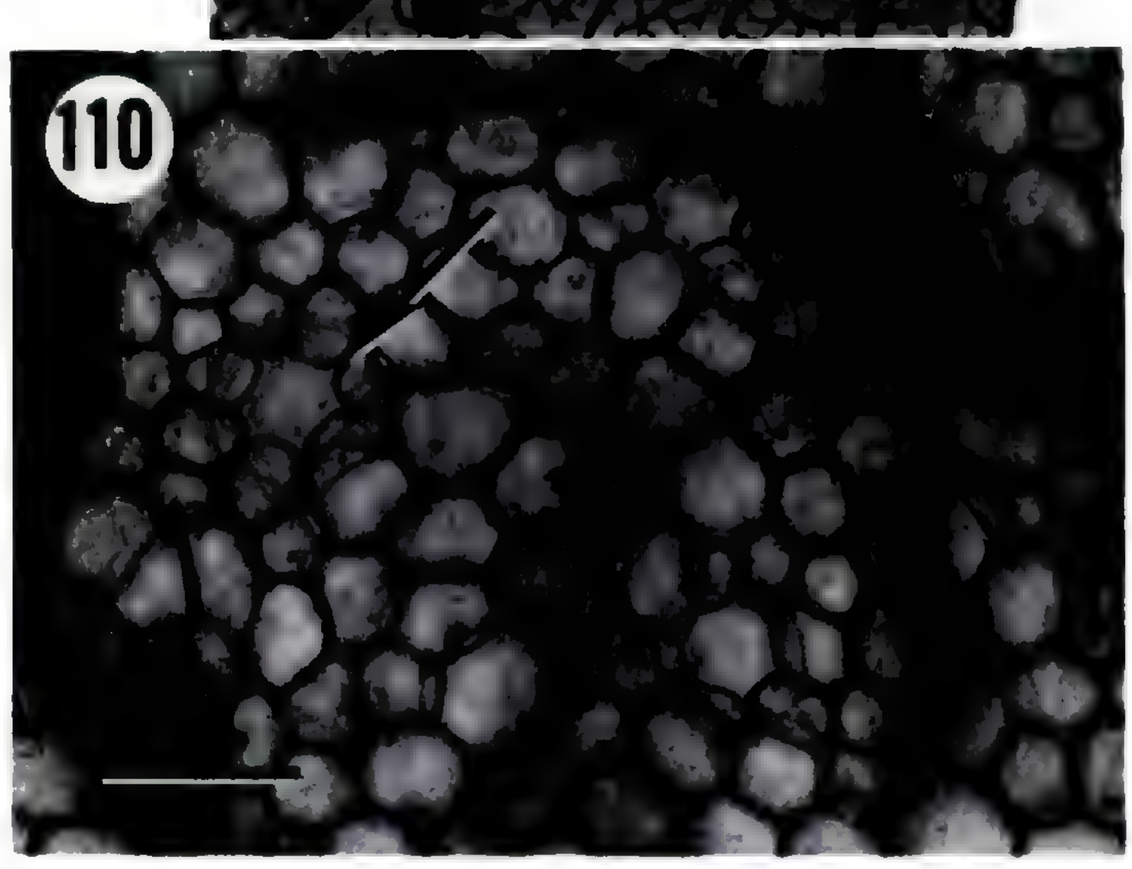
S. bacciforme (L.) Webst., Ceylon: *Wheeler 12034* (DAV). Figures 106, 107.

S. thesioides Hj. Eichl., Australia: South Australia, *Lothian 3234* (UC).

Leaves nanophylls, symmetrical, obovate; apex rounded, mucronate; base obtuse to rounded; organization of venation first rank; marginal ultimate venation incomplete; terminal tracheids normal (*S. thesioides*) or swollen (*S. bacciforme*); bundle sheath of higher order veins parenchymatous; stomata brachyparacytic or the subsidiary cells extending beyond the guard cells at one end only (Fig. 96); epidermis of *S. thesioides* containing groups of sclerified, papillate cells.

My observations of the epidermis of *S. bacciforme* agree with those of Raju and Rao (1977).





FIGURES 105–110. Leaves of *Reverchonia, Synostemon,* and *Uapaca.*—105. *Reverchonia arenaria.*—106, 107. *Synostemon bacciforme.*—108. *Uapaca guineensis.*—109. *U. heudelotii.*—110. Adaxial epidermis of *U. nitida,* with tanniniferous epidermal cells (arrow). Bars equal 1 cm in Figure 108; 5 cm in Figure 107; 1 mm in Figures 105, 106, 109; and 100 μm in Figure 110.

In contrast to the Securineginae, the Flueggeinae appear to form a closely knit group. *Flueggea, Margaritaria,* and *Richeriella,* the more primitive genera in the subtribe, have very similar leaf architecture and epidermal morphology. The more primitive sections of *Phyllanthus* that I examined, e.g., *Anisonema, Cicca,* and *Floribundi,* share many features with these three genera.

Apparently the shift within *Phyllanthus* to phyllanthoid branching (Webster, 1956, 1967), in which determinate, plagiotropic lateral branchlets mimic pinnate leaves, has led to an adaptive radiation into a variety of habitats with an attendant radiation in foliar morphology. The leaf architectural diversity within *Phyllanthus* and its closely related segregates, *Breynia, Glochidion, Sauropus, Synostemon,* and (probably) *Rev-*

erchonia (Webster, 1967; Webster & Miller, 1963) equals that of the rest of the subfamily, reflecting this radiation. Still, certain patterns can be detected. All these genera, with the exception of the herbaceous *Reverchonia,* share a similar stomatal development pattern, in which the divisions giving rise to the subsidiary cells and the guard mother cell exhibit a certain flexibility, giving rise to paracytic, brachyparacytic, and intermediate stomata on the same leaf (Fig. 96). As Webster (1956, 1957, 1958) and Raju and Rao (1977) demonstrated, the herbaceous taxa within this plexus, which are not closely related to each other, generally bear aniso- or anomocytic stomata, suggesting that the latter pattern in *Reverchonia* results from convergence. Also, the similarity of *Breynia, Glochidion,* and *Sauropus* suggests that they may belong to a single line derived from the more central *Phyllanthus* subgenera. The taxonomist interested in studying this group in detail should find leaf morphology a rich source of information.

HYMENOCARDIEAE (MUELL. ARG.) HUTCH.

Hymenocardia Wall. ex Lindl. (OTU 89)
H. acida Tul., Ghana: *Enti R775* (RSA).
H. laotica Gagnep., Indochina: *Thorel 1989* (UC).
H. lyrata Tul., Ivory Coast: *Leeuwenberg 2987* (UC).
H. mollis Pax, Tanganyika: *Tanner 5258* (UC). Figure 111.
H. wallichii Tul., Burma: *Dickason 6879* (RSA). Figure 112.

Leaves microphylls, symmetrical, ovate, elliptic, or obovate; apex acuminate, acute, or obtuse; base acute, obtuse, or rounded; organization of venation low fourth rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; unicellular trichomes typically above and beneath midrib and secondaries, in some species also beneath other veins, abaxially in junctions of midrib and secondaries, scattered on abaxial epidermis, or none; sessile, disk-shaped glands somewhat sunken in pits on the abaxial epidermis.

My anatomical observations agree with those of Rothdauscher (1896), Gaucher (1902), and Pax and Hoffmann (1922).

The leaf morphology of *Hymenocardia* reveals little about its relationships within the Phyllanthoideae, although the high rank of the leaves suggests proximity to the Phyllantheae. This is in accord with its wood, which is of the *Glochidion* type (Metcalfe & Chalk, 1950). Only *Didymocistus* bears similar sunken disk-shaped glands, suggesting that these genera are related.

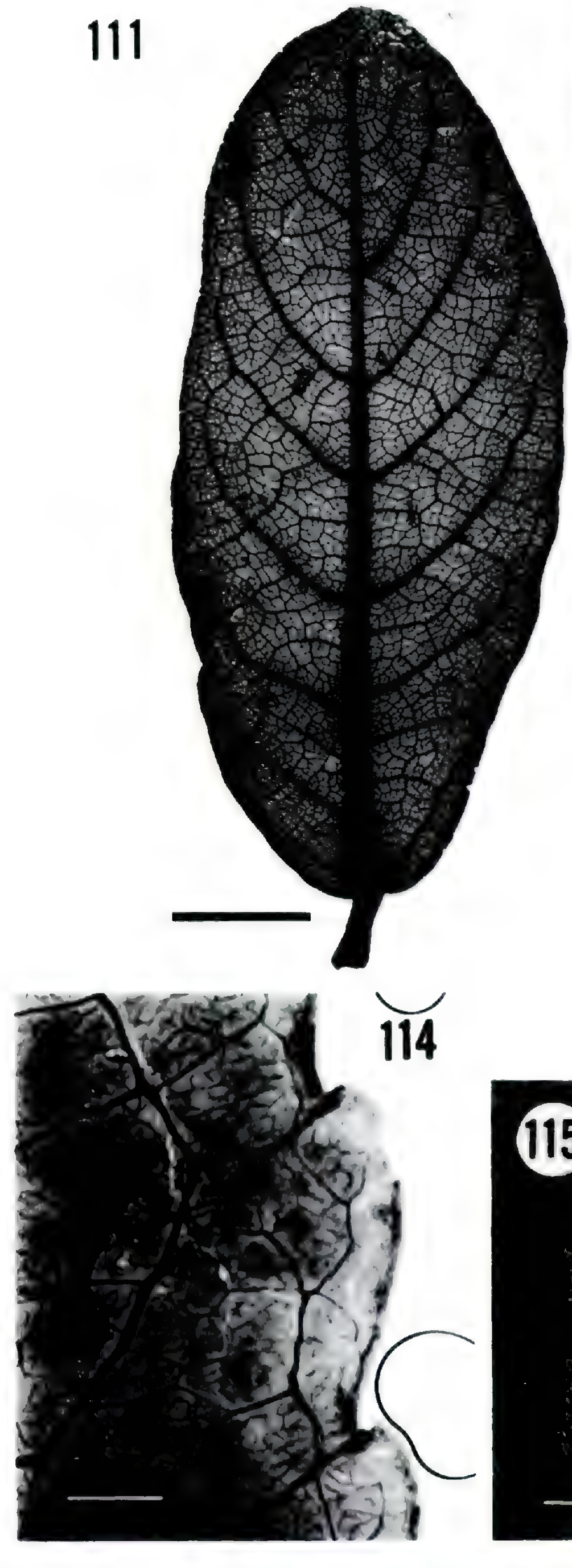
Airy Shaw (1965) recognized for *Hymenocardia* a distinct family related to the Ulmaceae on the basis of the winged fruits and pollen that closely resembles *Celtis.* The leaves of *Hymenocardia* are of much lower rank than is typical of the Ulmaceae and have symmetrical bases in contrast to *Celtis* and many other members of the Ulmaceae. Nothing in its foliar morphology suggests that *Hymenocardia* is out of place in the Euphorbiaceae, and both wood anatomy (Metcalfe & Chalk, 1950) and chromosome numbers (Mangenot & Mangenot, 1958; Webster & Ellis, 1962) support its retention.

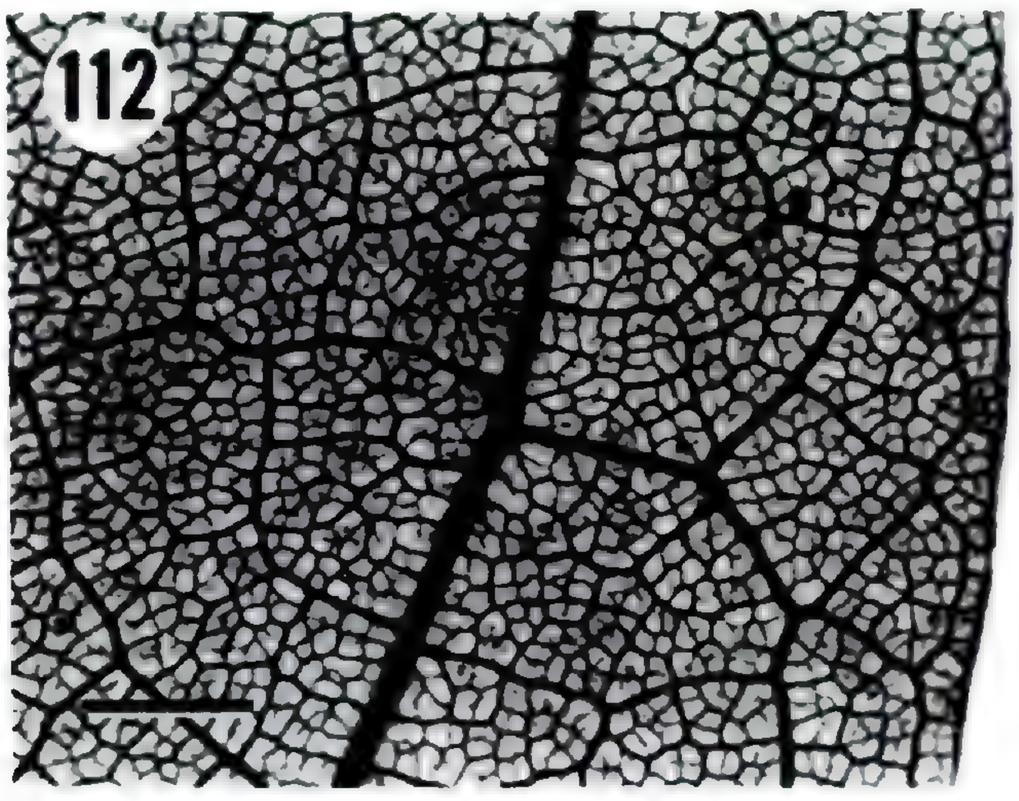
UAPACEAE (MUELL. ARG.) HUTCH.

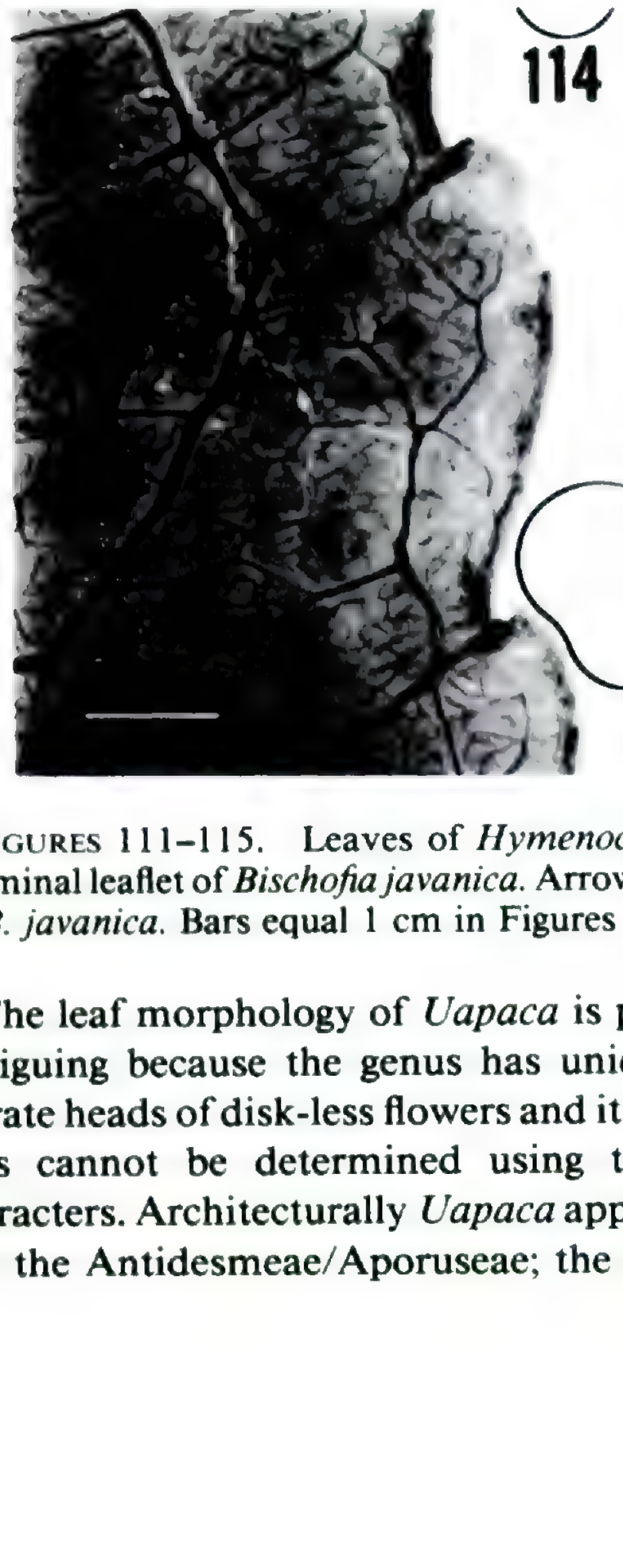
Uapaca Baill. (OTU 88)
U. guineensis Muell. Arg., Nigeria: *Ujor FHI 26153* (DAV), Liberia: *Voorhoeve 771* (UC). Figure 108.
U. heudelotii Baill., Nigeria: *Taylor FHI 31132* (DAV), Cameroons: *Bereteler et al. 2541* (UC), *Zenker 59* (UC). Figure 109.
U. nitida Muell. Arg., Rhodesia: *Rodin 4397* (UC). Figure 110.
U. sansibarica Pax, Nyasaland: *Brass 17466* (UC).
U. togoensis Pax, Nigeria: *Onochie FHI 32206* (DAV).

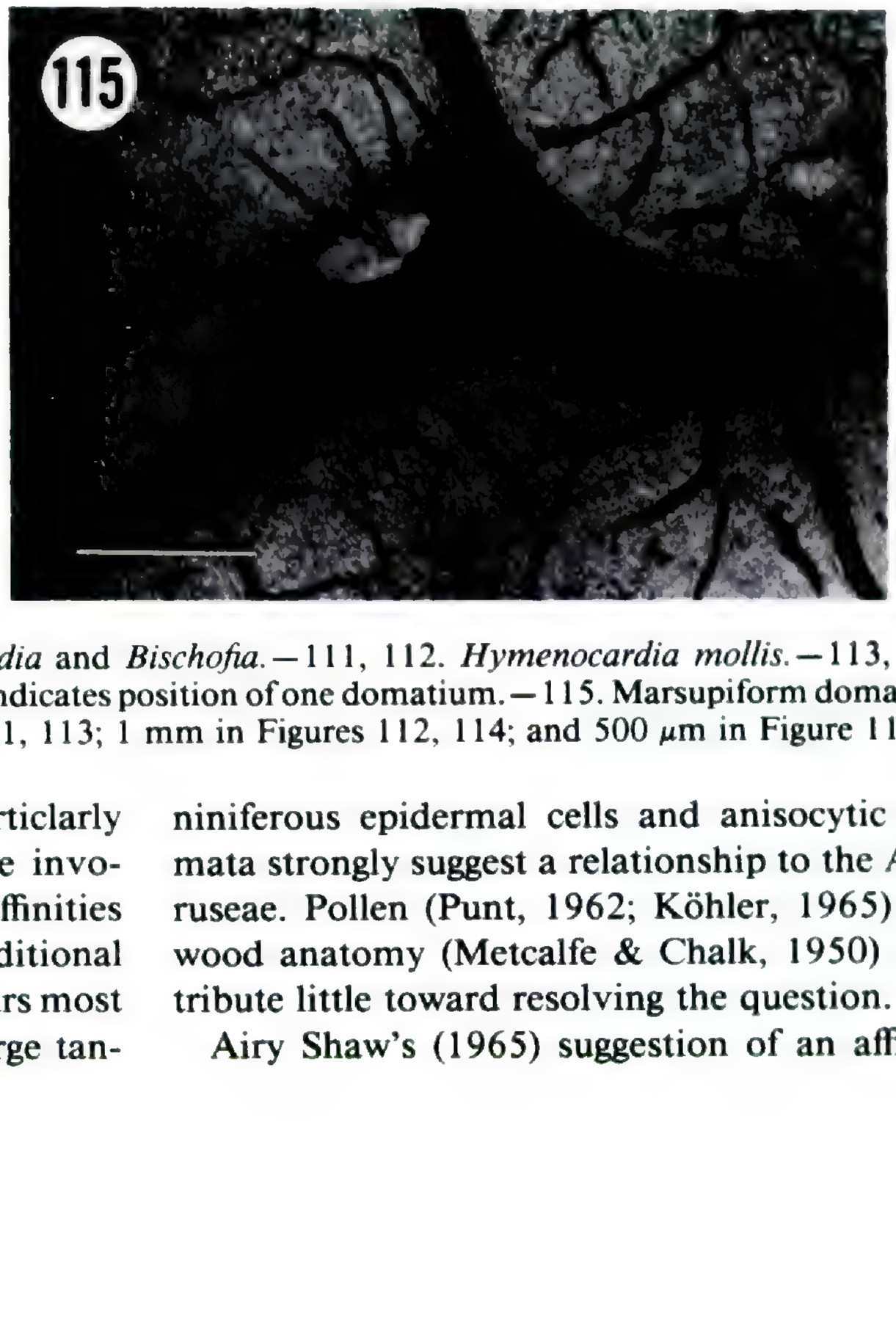
Leaves microphylls to mesophylls, symmetrical, obovate to oblanceolate; apex obtuse to rounded; base acute-cuneate; organization of venation mid third rank; marginal ultimate venation incomplete or partially looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata anisocytic; trichomes beneath veins (*U. sansibarica, U. togoensis*) or none; elongate tanniniferous cells originating in the epidermis and running through the mesophyll; tanniniferous cells in epidermis.

My anatomical observations generally agree with those of Gaucher (1902) and Comyn (1947), except that neither of them reported the large spherical tanniniferous cells in the epidermis. Comyn's (1947) illustrations of stomata from several species show the guard cells surrounded by a single subsidiary cell, a pattern that is known only from a few ferns (Fryns-Claessens & van Cotthem, 1973).









FIGURES 111–115. Leaves of *Hymenocardia* and *Bischofia*.—111, 112. *Hymenocardia mollis*.—113, 114. Terminal leaflet of *Bischofia javanica*. Arrow indicates position of one domatium.—115. Marsupiform domatium of *B. javanica*. Bars equal 1 cm in Figures 111, 113; 1 mm in Figures 112, 114; and 500 μm in Figure 115.

The leaf morphology of *Uapaca* is particlarly intriguing because the genus has unique involucrate heads of disk-less flowers and its affinities thus cannot be determined using traditional characters. Architecturally *Uapaca* appears most like the Antidesmeae/Aporuseae; the large tanniniferous epidermal cells and anisocytic stomata strongly suggest a relationship to the Aporuseae. Pollen (Punt, 1962; Köhler, 1965) and wood anatomy (Metcalfe & Chalk, 1950) contribute little toward resolving the question.

Airy Shaw's (1965) suggestion of an affinity

between *Uapaca* and the Anacardiaceae gains no support from foliar morphology. Anacardiaceae leaves typically are pinnately compound and exhibit distinct tendencies for the secondary veins to thin markedly at the margin and for the tertiary veins to thin markedly between the secondaries (J. Wolfe, pers. comm.). *Uapaca* shares none of these characteristics and also has higher venation that branches less than is typical of the Anacardiaceae (pers. observ.). Furthermore, Anacardiaceae generally have anomocytic stomata (Metcalfe & Chalk, 1950).

BISCHOFIEAE (MUELL. ARG.) HURUSAWA

Bischofia Bl. (OTU 91)

B. javanica Bl., Philippines: Mindanao, *Elmer 13895* (UC), Luzon: *Elmer 15228* (UC), U.S.A.: cult. California, *Reid s.n.* (DAV 88589). Figures 113–118.

Leaves trifoliolate, mesophylls; leaflets symmetrical above the base, obovate; apex obtuse to rounded; base obtuse, symmetrical on terminal leaflet, asymmetrical on lateral leaflets; organization of venation second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic; marsupiform domatia abaxially in junctions of midrib and secondaries and secondaries and tertiaries; irregularly shaped secretory cells in epidermis.

My observations agree with those of Rothdauscher (1896), Gaucher (1902), Penzig and Chiabrera (1903), and Raju and Rao (1977).

The teeth of *Bischofia* are traversed by a single vein that is shifted toward the sinus and ends with a flared tip below a clear, flame-shaped, deciduous glandular seta, also shifted toward the sinus (Figs. 114, 116–118). They are thus best interpreted as modified theoid teeth (Hickey & Wolfe, 1975). The teeth are concave on the upper side, convex on the lower side, with a rounded apex and rounded sinus. The axis of the tooth forms an angle of about 15° to the tangent. The teeth are regularly distributed along the upper two-thirds of the margin.

Within the Phyllanthoideae, the compound leaves and marsupiform domatia of *Bischofia* are unique. Airy Shaw (1967) pointed out that the terminal petiolule is longer than the lateral ones, suggesting that the leaf is basically pinnately rather than palmately compound, having become trifoliolate through loss of leaflets. In further support of his hypothesis, he cited a specimen bearing a pinnately 5-foliolate leaf and previous reports of young shoots with 5-foliolate leaves. Other genera of the Euphorbiaceae have compound leaves, but these are apparently palmate. This evidence would seem to support his earlier proposal of the family Bischofiaceae, to be near the Staphyleaceae because of supposed similarity in habit and foliage between *Bischofia* and *Tapiscia* (Airy Shaw, 1965).

The bulk of the evidence suggests otherwise. The floral morphology of *Bischofia* and the Staphyleaceae is completely different (Webster, 1967), as is the wood anatomy (W. J. Hayden, pers. comm.). Significantly, *Bischofia* has pendent, anatropous, bitegmic, crassinucellate ovules, with the micropyle roofed by a placental obturator (Bhatnagar & Kapil, 1974), a suite of characteristics that is diagnostic of the Euphorbiaceae (Webster, 1967) and not found in the Staphyleaceae (Davis, 1966). Foliar similarity is only superficial. Rather than theoid teeth, *Tapiscia* and other staphyleaceous genera have cunonioid teeth, in which the vein leading into the tooth forks, with one branch ending in a knot in the sinus and the other continuing into the tooth (Hickey & Wolfe, 1975 and pers. observ.). Further, in *Tapiscia* leaves, the venational organization is of higher rank than in the *Bischofia,* and the former have semicraspedodromous venation and anisocytic stomata (pers. observ.).

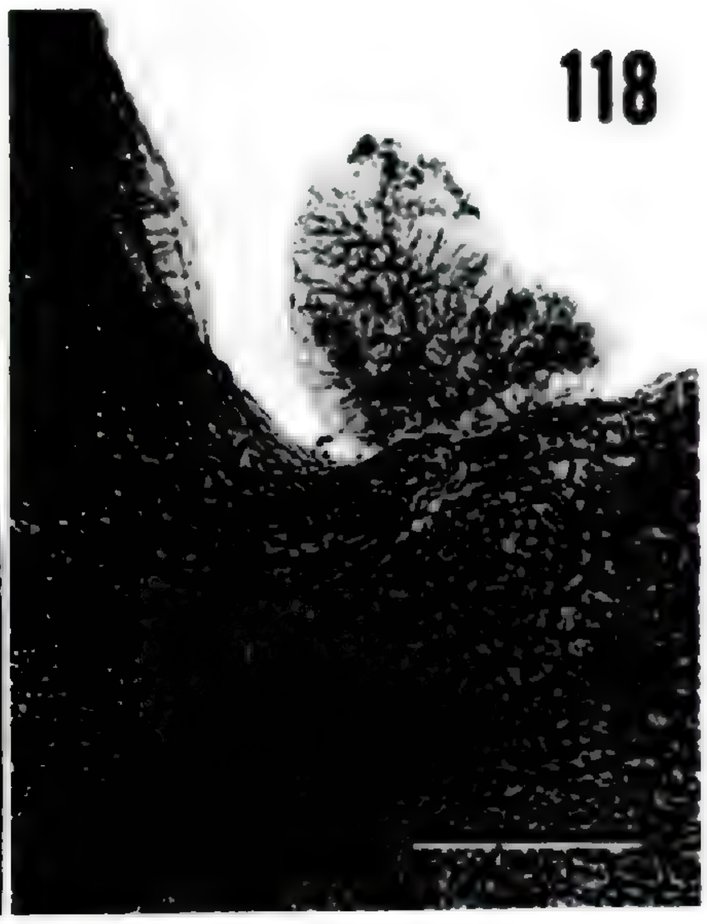
Based on this evidence, *Bischofia* is probably best placed in a separate tribe in the Phyllanthoideae, as originally proposed by Hurusawa (1954) and accepted by Webster (1975). Both phenetic and cladistic analyses of leaf characters emphasize the isolation of *Bischofia* (Levin, 1986 and in press).

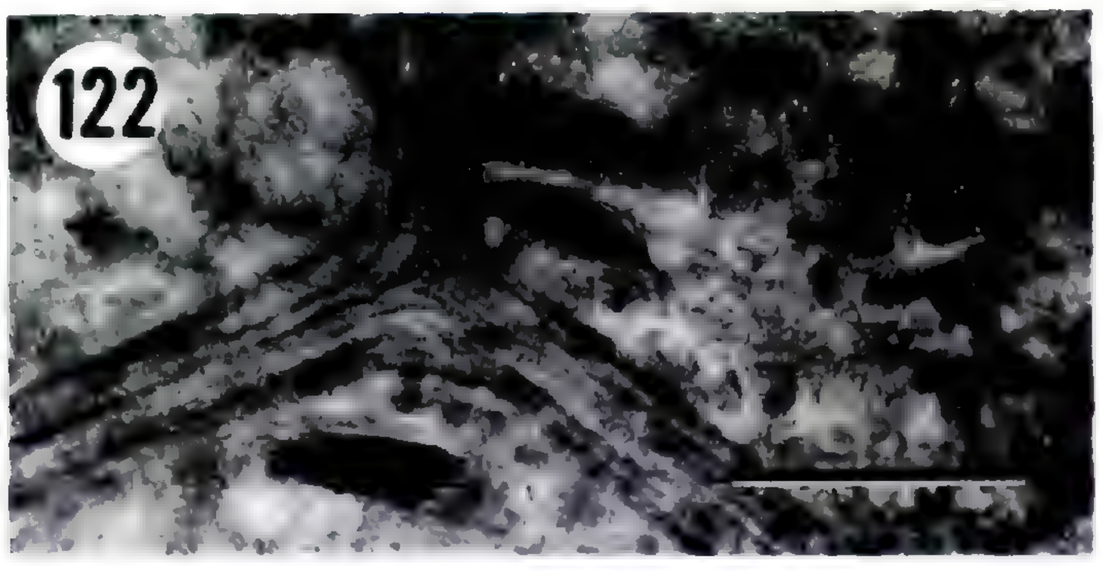
GENERA OFTEN INCLUDED IN THE EUPHORBIACEAE BUT EXCLUDED BY WEBSTER (1975)

Martretia Beille (OTU 92)

M. quadricornis Beille, Congo: *Corbisier-Boland 1391* (MO), Ivory Coast: *Leeuwenberg 2697* (UC). Figures 119, 120.

Leaves large microphylls or small mesophylls, symmetrical, narrow elliptic; apex acute; base acute; organization of venation mid second rank; marginal ultimate venation looped; terminal tracheids normal; bundle sheath of higher order veins parenchymatous; stomata paracytic.





FIGURES 116–122. Leaves of *Bischofia, Martretia,* and *Paradrypetes.*—116, 117. Teeth of *Bischofia javanica,* with and without deciduous seta.—118. Tooth of *B. javanica.*—119, 120. *Martretia quadricornis.*—121. *Paradrypetes ilicifolia.*—122. Raphides in mesophyll of *P. ilicifolia.* Bars equal 1 cm in Figures 119, 121; 1 mm in Figure 120; 500 μm in Figures 116, 117; and 150 μm in Figures 118, 122.

The foliar morphology of *Martretia* fits well within the Phyllanthoideae, and is most similar to *Actephila* (Levin, 1986 and in press), which share the straight-sided intercostal areas with frequent intersecondaries and reticulate tertiaries. However, the false partition in the fruit (Pax & Hoffmann, 1922) and atriate apertures in the pollen (Punt, 1962; Köhler, 1965) would be unique within the Phyllanthoideae. Clearly more information on this monotypic genus is required before its relationships will be understood.

Paradrypetes Kuhlm.

P. ilicifolia Kuhlm., Brazil: Tombos, *Barreto 1663* (F). Figures 121–123.

Leaves simple, mesophylls, symmetrical, obovate; apex obtuse; base acute; margin with spinose teeth; organization of venation low third rank, pinnate, weakly brochidodromous; primary vein stout, straight; secondary veins arising at a wide acute angle, the angle more or less uniform, their thickness moderate, course curved abruptly, loop-forming branches joining acutely and accompanied by uniform tertiary loops; intersecondary veins composite, zig-zag, one present in each intercostal area and running its length; tertiaries originating from secondaries at acute angles, weakly percurrent, branching to form intersecondaries, essentially parallel to the midrib; fourth order veins orthogonal, their size moderate; fifth and sixth order veins random, their sizes moderate; highest vein order sixth; marginal ultimate venation fimbriate; areole development imperfect, arrangement random, shape triangular to polygonal, size moderate; veinlets simple or branched once; terminal tracheids normal; bundle sheath of higher order veins sclerified; epidermal cells isodiametric, arrangement random, anticlinal walls curved; stomata abaxial, orientation random, stomatal index about 12%, basically paracytic, but each subsidiary cell divided again by one or more wall at right angles to the guard cells, thus similar to the laterocytic type of den Hartog and Baas (1978); trichomes none; crystals present as raphides in abundant idioblasts just below the epidermis.

The teeth of *Paradrypetes* are spinose, traversed by a single vein terminating in a point at the tooth apex. Both sides of the tooth are straight, the apex acute, and the sinus rounded. The axis of the tooth forms an angle of about 25° to the tangent. The teeth are distributed very irregularly along the upper two-thirds of the margin.

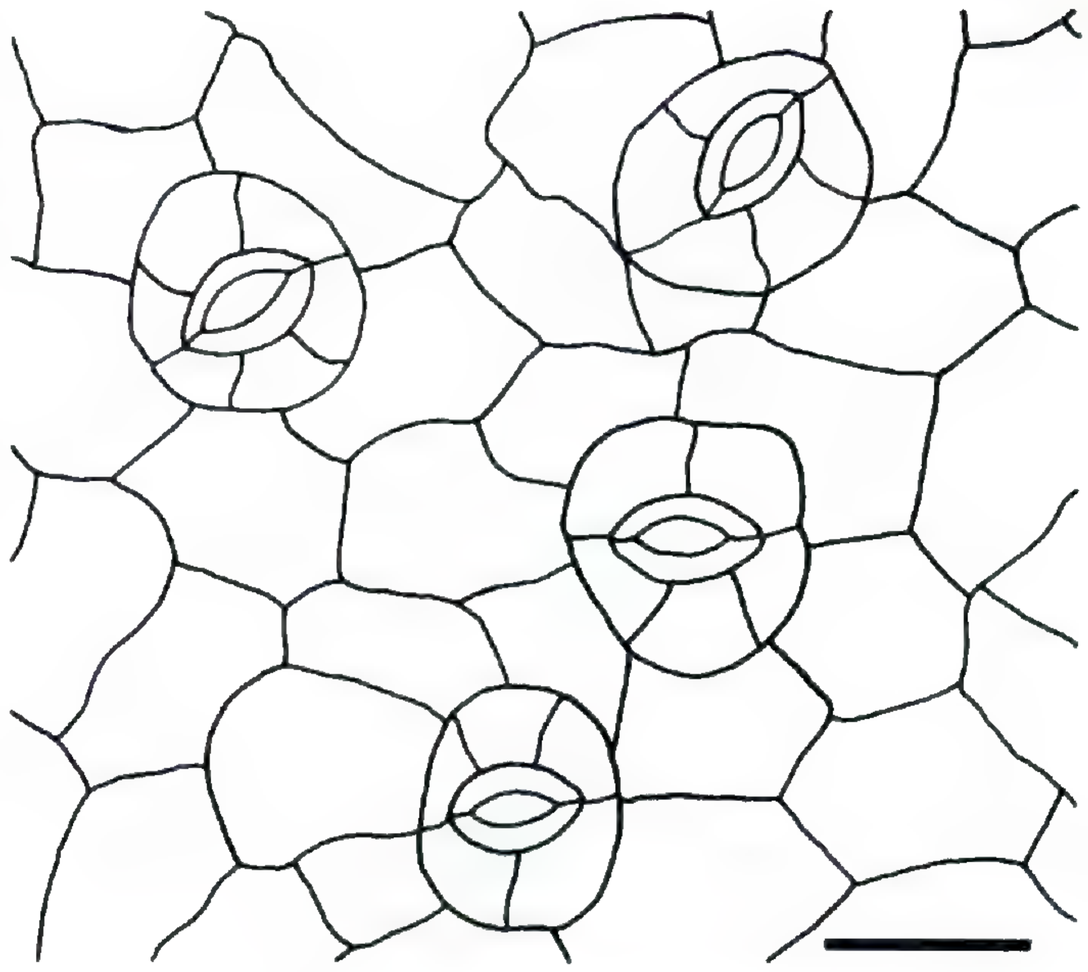


FIGURE 123. Abaxial epidermis of *Paradrypetes ilicifolia*. Bar equals 100 μm.

Paradrypetes, as the name suggests, was considered by Kuhlmann (1935) to be closely related to *Drypetes*. However the foliar morphology of *Paradrypetes*, of which my observations agree with those of Milanez (1935), would make this genus quite anomalous in the Phyllanthoideae and even in the Euphorbiaceae. The most obvious discrepancies are the long, zig-zag intersecondaries, unlike any that I have seen in the subfamily, the tertiaries parallel to the midrib, and the raphides. I have never observed raphides in any phyllanthoides; Gaucher (1902) firmly stated that raphides are never found in the Euphorbiaceae. Milanez (1935) reported that raphides are abundant in every part of the plant, including the embryo. I agree with Webster (1975) that the resemblance between *Paradrypetes* and *Drypetes* is superficial, and that the former should be excluded from the Euphorbiaceae. There are few families with both stipules and raphides (Metcalfe & Chalk, 1950); further study may reveal the proper relationships of this monotypic genus.

RELATIONSHIPS OF THE EUPHORBIACEAE

The foliar morphology of the Phyllanthoideae helps narrow the choice of hypotheses regarding the relationships of the Euphorbiaceae. Particularly significant are the basically theoid teeth of *Bischofia*, *Drypetes*, and *Putranjiva*. Hayden (1980) reported teeth intermediate between the theoid and violoid types in *Choriceras* (Oldfieldioideae), and Hickey and Wolfe (1975), who presumably examined the uniovulate subfamilies

almost exclusively, characterized the Euphorbiaceae as having violoid teeth. This series can be interpreted as a parallel to the shift from theoid to violoid teeth that Hickey and Wolfe (1975) inferred to have occurred in the Violales, supporting the suggestions of Takhtajan (1980) and Thorne (1976) that the two groups share common ancestry.

The Rosidae typically have teeth assigned by Hickey and Wolfe (1975) either to the cunonioid type or its presumed derivative, the rosid type. These types differ from the theoid type in their venation and non-deciduous glandular apex. In contrast, teeth of some Celastrales, particularly members of the Aquifoliaceae and Celastraceae, bear deciduous setae, although these teeth differ from typical theoid teeth in that the former have the apex strongly turned inward toward the sinus whereas the latter are essentially symmetrical. Hickey and Wolfe (1975) originally interpreted the teeth of the Celastrales as modifications of the theoid tooth type, and largely on that basis transferred this order from the Rosidae, in which it is included in the systems of Cronquist (1981) and Takhtajan (1980), to the Dilleniidae. More recently, teeth of the celastroid type have been found in *Brexia* and related genera, which are placed in or near the Saxifragaceae by most authors. Hickey and Wolfe now view the type of tooth found in *Brexia* and the Celastrales as a modification of the similarly asymmetrical cunonioid tooth, and agree that the Celastrales belong in the Rosidae (L. Hickey and J. Wolfe, pers. comm.).

In light of the proposed relationship between the Euphorbiales and the Celastrales, the asymmetrical teeth of *Bischofia* deserve particular attention. Although they, like the teeth of *Brexia* and the Celastrales, have the vein and seta shifted toward the sinus, the degree of shifting is much less than is typical of brexioid/celastroid teeth (Levin, pers. observ.). Tooth morphology, therefore, supports the proposed dilleniid relationships of the Euphorbiaceae somewhat more strongly than the relationship to the Celastrales, but the latter possibility remains. A relationship between Euphorbiaceae and the Geraniales appears much less probable than either of these other possibilities.

Venation patterns provide additional evidence in this regard. In *Drypetes* and many entire-leaved phyllanthoids, the basal secondary veins arise at a significantly different angle from the other secondaries. This pattern suggests either incipient or vestigial actinodromy (Hickey & Wolfe, 1975; Hayden, 1980) and is also found in various primitive Violaceae and Flacourtiaceae (Hickey & Wolfe, 1975). Better developed actinodromy is common in other subfamilies of the Euphorbiaceae, and characterizes a group that Hickey and Wolfe (1975) referred to as the "palmate Dilleniidae," consisting of the Violales, Malvales, and related orders. Although palmate venation occurs sparingly in some rosid orders, including the Geraniales, leaves of the Rosidae typically have pinnate venation and are commonly pinnately compound (Hickey & Wolfe, 1975). Among the Phyllanthoideae (and, in fact, the entire Euphorbiaceae) the only genus with any suggestion of pinnately compound leaves is *Bischofia*.

Thus neither venation nor tooth morphology alone allows the possibility of rosid relationships to be eliminated for the Euphorbiaceae. Taken together, however, these aspects of leaf architecture suggest that the dilleniid relationship is more tenable. The relationship to the Geraniales is unlikely given the theoid teeth of the Phyllanthoideae; although the Celastrales have somewhat similar teeth, differences in the teeth apparent upon close comparison and the suggestion of incipiently actinodromous venation in the Phyllanthoideae make a relationship to this order doubtful. However, the Euphorbiaceae share with the Violales and Malvales both basically similar teeth and venation patterns.

CONCLUSIONS

Leaf architecture and epidermal morphology vary in a taxonomically useful way in the Phyllanthoideae. Most tribes recognized by Webster (1975) appear to be relatively homogeneous and well defined, with most exceptions being tribes that contain genera that have become either herbaceous or highly xerophytic. Within the subfamily (but excluding herbaceous or highly xerophytic genera), venational organization is of lowest rank in those tribes generally agreed to have the most primitive flowers, i.e., the Wielandieae and Amanoeae, and of highest rank in putatively more derived tribes, e.g., Phyllantheae and Hymenocardieae, a pattern that conforms to Hickey's (1971, 1977) generalization that the level of organization increases evolutionarily. Cladistic and phenetic analyses of the foliar morphology presented elsewhere (Levin, 1986 and in press) clarify additional evolutionary patterns, such as the closeness of the Antidesmeae, Apo-

ruseae, and Spondiantheae, and the proximity of *Astrocasia, Andrachne,* and the Phyllantheae.

In addition to confirming the general aspects of Webster's (1975) classification indicated above, foliar morphology indicates some genera whose relationships require reconsideration. Prominent among these are *Celianella, Croizatia, Didymocistus, Jablonskia* (= *Securinega congesta*), and *Neowawraea,* all of which are poorly known and/or recently described. The relationships between *Amanoa* and *Actephila* may also deserve examinaton, because the leaves of these genera differ considerably from each other. Finally, attention should be paid to the suggestion, based primarily on unusual epidermal characteristics but supported by architecture, of a relationship between *Uapaca* and the Aporuseae.

Leaf architecture also proves phylogenetically valuable at higher levels. The presence of theoid teeth and suggestion of vestigial or incipient actinodromy in the most primitive subfamily of the Euphorbiaceae argue for placement of the family in the vicinity of the Violales in the Dilleniidae. The most popular alternative, that of rosid affinities, gains little support from leaf architecture.

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SYSTEMATIC FOLIAR MORPHOLOGY OF PHYLLANTHOIDEAE (EUPHORBIACEAE). II. PHENETIC ANALYSIS[1]

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ABSTRACT

Leaf architectural and cuticular characters in the Phyllanthoideae (Euphorbiaceae) were analyzed using Similarity Graph Clustering. The resulting groups and their similarity relationships correspond remarkably well to classifications based on more traditional taxonomic characters. Exceptions generally appear to be either cases in which other evidence also suggests that previous classifications are invalid or in which total similarity could be expected to be a poor indicator of relationship. Obtaining such clear results in a group not known for having diagnostic leaf characteristics indicates the considerable potential foliar morphology has for classification of modern and fossil angiosperms.

This paper reports the first numerical analysis of leaf architectural and cuticular features of a related group of extant flowering plants. This is part of a project undertaken both to test the systematic potential of leaf characters at higher taxonomic levels and to explore the contribution of foliar morphology to the phylogeny of the Euphorbiaceae. Earlier studies (Dolph, 1976; Hill, 1980) have tested foliar character sets by attempting to correctly identify leaves taken from randomly selected, usually unrelated plants. For example, Hill collected five leaves each from 20 species of woody plants growing in a botanic garden. His sample included 19 genera from 12 families. Although both he and, to a lesser extent, Dolph achieved their stated goal of taximetrically grouping together leaves taken from the same species, neither was able to recognize any higher taxa using their methods and character sets.

I instead chose to test the systematic usefulness of a leaf character set in a natural group by comparing the results of numerical analysis of leaf characters with recent classifications based on more traditional sources of systematic data. I selected for study the Phyllanthoideae, putatively the most primitive subfamily of the Euphorbiaceae, because the long history of systematic interest in the family has resulted in a series of infrafamilial classifications based on characteristics drawn from a wide variety of organs (see reviews in Webster, 1967 and Hutchinson, 1969) and because of the broader phylogenetic significance of the subfamily in clarifying the relationships of the Euphorbiaceae. That the leaves of the Phyllanthoideae are relatively nondescript makes analysis of this group of additional interest. The recent treatment by Webster (1975; see Table 1), who integrated evidence from floral morphology, palynology, cytology, and wood anatomy, serves as the principal classification with which to compare the foliar analysis.

I derived leaf architectural characters from the system proposed by Hickey (1973). Although the use of this character set for numerical analysis has been criticized because many characters do not have equidistant quantitative states (Hill, 1980), the characters have been shown to be of systematic importance at higher taxonomic levels (Hickey & Wolfe, 1975). Cuticular characters were selected from the list prepared by Stace (1965; see also Dilcher, 1974). In another paper (Levin, 1985), I discussed the characters and their states and described the leaves of the 51 genera in the Phyllanthoideae that I examined. In a future paper (Levin, in press), I will present the results of a cladistic analysis of the same data set.

MATERIALS AND METHODS

DATA GATHERING PROCEDURES

The taxa included in this study are listed in Table 1, along with the numbers I assigned to them for convenience of representation in Figures 1–6. For reasons that I explain below, I have deleted from the list all the taxa with phyllan-

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TABLE 1. Taxa includes in study and numbers assigned to OTUs. Classification follows Webster (1975).

Number	Taxon
	WIELANDIEAE
1	*Wielandia*
2	*Astrocasia*
9	*Blotia*
5	*Discocarpus*
3	*Heywoodia*
4	*Lachnostylis*
13	*Pentabrachium*
8	*Petalodiscus*
6	*Savia* sect. *Heterosavia*
7	*S.* sect. *Savia*
	AMANOEAE
10	*Amanoa*
11	*Actephila* group 1: *A. anthelminthica, A. nitida*
12	*A.* group 2: *A. excelsa*
93	*Croizatia*
	BRIDELIEAE
14	*Bridelia* group 1: sects. *Micrantheae* pro parte, *Scleroneurae* pro parte
15	*B.* group 2: sect. *Cleistanthoideae*
	B. group 3: sects. *Micranthae* pro parte, *Scleroneurae* pro parte, *Stipulares*
17	*Cleistanthus acuminatissimus*
18	*C.* sect. *Stipulati*
19	*C.* sects. *Ferruginosi, Pedicellati*
20	*Cleistanthus* sect. *Chartacei*
21	*C.* sect. *Cleistanthus*
22	*C. saichikii*
23	*C.* sect. *Australes*
24	*C.* sect. *Leiopyxis*
	DICOELIEAE
25	*Dicoelia*
	PORANTHEREAE
26	*Andrachne* sects. *Arachne, Phyllanthidia*
27	*A.* sect. *Phyllanthopsis*
	SPONDIANTHEAE
28	*Spondianthus*
	ANTIDESMEAE
29	*Antidesma* sects. *Roxburghiana, Venosa* pro parte
30	*A.* sects. *Laciniata, Venosa* pro parte
31	*A.* sect. *Tetrandra*
32	*A.* sect. *Montana*
33	*A.* sect. *Velutinosa*
34	*A.* sect. *Ghaesembilla*
35	*Celianella*
36	*Hyeronima*
37	*Leptonema*
38	*Thecacoris*

TABLE 1. Continued.

Number	Taxon
	APORUSEAE
39	*Aporusa*
40	*Ashtonia*
41	*Baccaurea* sects. *Everettiodendron, Calyptroon*
42	*B.* sect. *Pierardia*
43	*B. Dubiae*
44	*B.* sect. *Isoandrion*
45	*Didymocistus*
46	*Maesobotrya*
47	*Protomegabaria*
48	*Richeria*
	DRYPETEAE
49	*Drypetes* sects. *Drypetes* pro parte, *Sphragidia* pro parte
50	*D.* sects. *Drypetes* pro parte, *Sphragidia* pro parte
51	*D.* sect. *Sphragidia* pro parte
52	*D.* sects. *Oligandrae* pro parte, *Stemonodiscus, Stenogynium, Stipulares* pro parte
53	*D.* sects. *Oligandrae* pro parte, *Stipulares* pro parte
54	*D.* sect. *Drypetes* pro parte
90	*Neowawraea*
55	*Putranjiva*
	PHYLLANTHEAE
	Securineginae
56	*Jablonskia*
57	*Keayodendron*
58	*Meineckia*
59	*Pseudolachnostylis*
60	*Zimmermannia*
	Flueggeinae
61	*Flueggea*
67	*Margaritaria*
	UAPACEAE
88	*Uapaca*
	HYMENOCARDIEAE
89	*Hymenocardia*
	BISCHOFIEAE
91	*Bischofia*
	INCERTAE SEDIS
92	*Martretia*

thoid branching, in which plagiotropic branch systems resemble pinnately compound leaves (OTUs 62–66 and 68–87). In all but a few cases, I studied cleared leaves of a minimum of 10% of the species of each genus. I then grouped the

TABLE 2. Characters and character states. See Hickey (1973), Dilcher (1974), and Levin (1985) for more explanation. The type of each character, and for ordered characters the value chosen for j, is indicated in parentheses.

1. Organization: Simple or Compound. (Simple)
2. Base Balance: Symmetrical or Asymmetrical. (Simple)
3. Margin: Entire, Entire or crenate, but with glands, or Toothed. (Ordered, 1)
4. Venation: Brochidodromous, Weakly brochidodromous, or Eucamptodromous. (Ordered, 1)
5. Primary size: Moderate, Stout, or Massive. (Ordered, 1)
6. Secondary angle: Narrow (<45°), Moderate, or Wide (>65°). (Ordered, 1)
7. Angle of basal secondaries, relative to adjacent secondaries: More acute, Similar, or More obtuse. (Ordered, 1)
8. Angle of lower secondaries, relative to middle secondaries: More acute, Similar, or More obtuse. (Ordered, 1)
9. Angle of upper secondaries, relative to middle secondaries: More acute, Similar, or More obtuse. (Ordered, 1)
10. Secondary course: Curved uniformly or Curved abruptly. (Simple)
11. Angle of secondary loops: Acute, Right, or Obtuse. (Ordered, 1)
12. Size of outer loops: Irregular, Uniform, Decreasing upwards, or Absent. (Ordered, 1)
13. Tertiary angle of origin, admedial: Acute, Right, or Obtuse. (Ordered, 1)
14. Teritary angle of origin, exmedial: Acute, Right, or Obtuse. (Ordered, 1)
15. Tertiary pattern: Ramified, Random reticulate, Orthogonal reticulate, Weakly percurrent, Strongly percurrent with angle to midrib oblique, or Strongly percurrent with angle to midrib predominantly right. (Ordered, 3)
16. Simple intersecondaries: Absent or Present. (Simple)
17. Composite intersecondaries: Absent, Infrequent (in fewer than 20% of intercostal areas), or Frequent (in more than 20% of intercostal areas). (Ordered, 1)
18. Intramarginal vein: Absent or Present. (Simple)
19. Higher order vein pattern: Ramified, All random, 4° orthogonal and higher orders random, or 4° and 5° orthogonal. (Ordered, 2)
20. Higher order vein size: 4° moderate and 5° heavy, All moderate, 4° moderate and 5° fine, or 4° and 5° fine. (Ordered, 2)
21. Highest order present: 4°, 5°, or 6°. (Ordered, 1)
22. Areole development: Incomplete, Imperfect, or Well-developed. (Ordered, 1)
23. Areole arrangement: Random or Ordered. (Simple)
24. Areole shape: Irregular or Regular. (Simple)
25. Areole size: Large, Medium, or Small. (Ordered, 1)
26. Veinlets: Absent, Simple, Branched 1–2×, or Branched 2–3×. (Ordered, 2)
27. Prismatic crystals in mesophyll: Absent or Present. (Simple)
28. Prismatic crystals with veins: Absent or Present. (Simple)
29. Druses in mesophyll: Absent or Present. (Simple)
30. Druses with veins: Absent or Present. (Simple)
31. Epidermal anticlinal walls, adaxial: Straight or Undulate. (Simple)
32. Epidermal anticlinal walls, abaxial: Straight or Undulate. (Simple)
33. Epidermal papillae: Absent or Present. (Simple)
34. Stomatal location: Abaxial only, Primarily abaxial but a few adaxial, or Approximately equal on both surfaces. (Ordered, 1)
35. Stomatal index (abaxial): <10%, 10–20%, or >20%. (Ordered, 1)
36. Stomatal type: Paracytic or Anisocytic. (Simple)
37. Water stomata: Absent or Present. (Simple)
38. Unicellular trichomes: Absent, Solitary, or Some tufted. (Ordered, 1)
39. Uniseriate, multicellular trichomes: Absent or Present. (Simple)
40. Peltate trichomes: Absent or Present. (Simple)
41. Filiform sclereids in mesophyll: Absent or Present. (Simple)
42. Tanniniferous epidermal cells: Absent or Present. (Simple)
43. Sclerified epidermal cells: Absent or Present. (Simple)

TABLE 2. Continued.

species into homogeneous groups, which generally correspond to sections or undivided genera. I treated each group as an operational taxonomic unit, or OTU, for this study. Details of the procedures I used for collecting and clearing the leaves and for selecting the OTUs have been published in another paper (Levin, 1986).

Table 2 lists the 43 characters I scored for each leaf. These characters and their states are described by Stace (1965), Hickey (1973), and Levin (1986). All are binary or multistate qualitative characters. The basic data matrix has been published elsewhere (Levin, 1986: table 1) and will not be reproduced here.

DATA-ANALYTIC METHOD

Rather than using a clustering method like UPGMA that merely indicates the level of similarity at which a taxon or group of taxa first joins

another taxon or group of taxa and expresses the results in the form of a dendrogram, I chose to use Similarity-Graph Clustering (SIMGRA). This method, because it does not force the results into a hierarchical form but instead shows all relationships at a given similarity level, summarizes the reticulate structure of the similarity matrix far more completely than do other clustering methods (Prance et al., 1969; Legendre & Rogers, 1972). The theoretical and mathematical frameworks of SIMGRA can be found in Estabrook (1966), Estabrook and Rogers (1966), Wirth et al. (1966), and Legendre and Rogers (1972), and other examples of its use in Prance et al. (1969), Rogers and Fleming (1973), and Duncan (1980). The explanation presented here is derived from these references.

The SIMGRA algorithm consists of two steps. First, a similarity measure is calculated for all pairs of objects (the OTUs in Table 1). The similarity measure used here is the generalized Simple Matching Coefficient of Estabrook and Rogers (1966). This is defined as:

$$S(a,b) = \frac{\sum_{k=1}^{n} S_k(a,b)}{n}$$

where S(a,b) is the similarity between any two OTUs a and b, $S_k(a,b)$ is the partial similarity between a and b for any character k, and n is the number of characters used to compare the OTUs. If OTUs a and b share the same state for character k, then $S_k(a,b) = 1$. If the two OTUs differ for character k, then one of three rules may be chosen by the taxonomist to calculate $S_k(a,b)$:

1. $S_k(a,b) = 0$ (simple character);
2. $S_k(a,b) = \frac{2(j + 1 - d)}{2j + 2 + dj}$ whenever $d \leq j$
   $= 0$ when $d > j$,

   where j is the maximum number of character states by which two OTUs may be separated and still be considered at all similar, and d is the distance apart that the two states are in a pre-specified ordering of the states (ordered character); or
3. $S_k(a,b)$ = arbitrary values assigned by the taxonomist in advance, by providng a matrix of values between 0 and 1 (matrix character).

Thus the partial similarities for both ordered and matrix characters involve subjective decisions on the part of the taxonomist. For the ordered characters in this study, I set the value of j for character k at the number of character states for that character less two or three; these values cause only the most extreme distances between character states to yield a partial similarity of 0. There were no matrix characters in this study. The type of each character and, for ordered characters, the value of j, are indicated in Table 2.

After an overall similarity value S(a,b) has been calculated for each pair of OTUs, the similarity values are examined in order of decreasing magnitude. At each level of similarity, a connection is formed between two OTUs if they are at least as similar as the specified level. A cluster is a group of OTUs for which there exists at least one continuous pathway of connections joining the OTUs. The procedure continues until all the OTUs belong to one cluster. In this study, I used the program SIMGRA by G. F. Estabrook (Univ. of Michigan) on an IBM 4341 at the University of California at Berkeley.

Results

During the SIMGRA analysis, clusters were formed and enlarged at 45 levels of similarity. I grouped these levels and summarized them in Figures 1–6. On each drawing the lowest similarity value at which connections were made (S), the levels summarized (L), and the number of OTUs that have not yet formed a connection with any other OTU (single member clusters or SMCs) are listed on the left side. Each OTU that has formed a connection with another is indicated by a number, as listed in Table 1. Connections formed at any of the similarity levels summarized are represented by dashed lines, connections formed at previous levels by solid lines. In the following discussion, clusters are referred to by the prefix "C-," followed by the lowest-numbered OTU belonging to the cluster. Within a cluster, tightly connected subsets of OTUs that are less tightly connected to other subsets are termed subclusters and referred to by the prefix "SC-," with the lowest-numbered OTU as the suffix. For highly connected groups, either clusters or subclusters, it is often inconvenient to show all the connections. Such a group of OTUs, therefore, is shown diagrammatically as a circle, with the OTUs forming the cluster representing by placing their numbers at the edge of the circle. The fraction in the center, in which the numerator equals the number of connections actually formed within the cluster and the de-

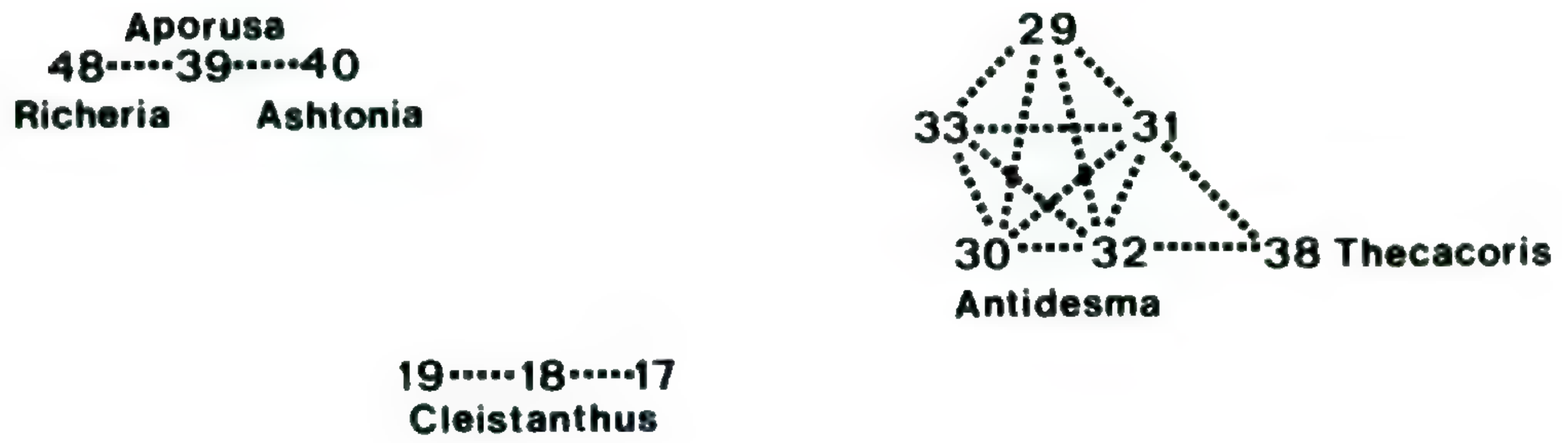

FIGURE 1. Clusters present in SIMGRA analysis at level II or similarity value 0.92000. In this and all following figures, OTUs are represented by numbers, as listed in Table 1. Dashed lines indicate connections formed between OTUs at any of the similarity levels summarized in the figure, thin solid lines indicate connections formed at previous levels, and thick solid lines indicate connections between circular subclusters. The lengths of lines reflect the constraints of two-dimensional representation and in no way indicate the degree of connectedness between the groups. See text for further explanation.

nominator equals the number of connections that are possible, indicates the connectedness of the cluster's members. Connections between circular subclusters, designated by the prefix "CSC-," are represented by a heavy solid line accompanied by a fraction that represents the degree of connectedness between the subclusters; again, the numerator of the fraction indicates the number of actual connections and the denominator equals the number of possible connections between the OTUs in the two subclusters. The length of the line bears no relationship to the connectedness between the groups.

Initially, I included all the OTUs for which I had data (Levin, 1985: table 1) except for *Lingelsheimia,* which I received after I had completed all the SIMGRA analysis. It immediately became clear that members of the Flueggeineae exhibited overwhelming convergence with other OTUs, completely obscuring relationships both within the subtribe and between the other OTUs. The foliar morphology of this species-rich group has apparently undergone an adaptive radiation, associated with the evolution of phyllanthoid branching, in which determinate lateral branchlets mimic pinnately compound leaves (Webster, 1956, 1967; Levin, 1985). Fortunately for the systematist, the more primitive members of the subtribe, *Flueggea, Margaritaria, Richeriella,* and a few species of *Phyllanthus,* retain the normal habit. I therefore removed the genera with phyllanthoid branching (*Breynia, Glochidion, Phyllanthus, Sauropus,* and *Synostemon*) from the analysis, leaving the 68 OTUs in Table 1.

After the first 11 similarity levels (Fig. 1), 19 OTUs have joined to form six clusters, and 49 OTUs remain as SMCs. The only large cluster, C-29, consists of *Thecacoris* (OTU 38) and a completely interconnected subcluster containing all but one section of *Antidesma.* The other clusters have only two or three members and are minimally connected. As Figure 1 indicates, the first-formed clusters generally consist of OTUs from a single genus or of closely related genera, which might be expected to be quite similar. Had *Lingelsheimia* been included in the analysis, it would have joined C-2 through a connection with *Zimmermannia* (60) at level 6.

The next seven levels, to S = 0.90000 (Fig. 2), see the formation of five new two-membered clusters and the enlargement of the earlier-formed clusters. Two new internal connections form in C-29, very tightly connecting *Thecacoris* to the other OTUs in the cluster. C-2 and C-61 join to

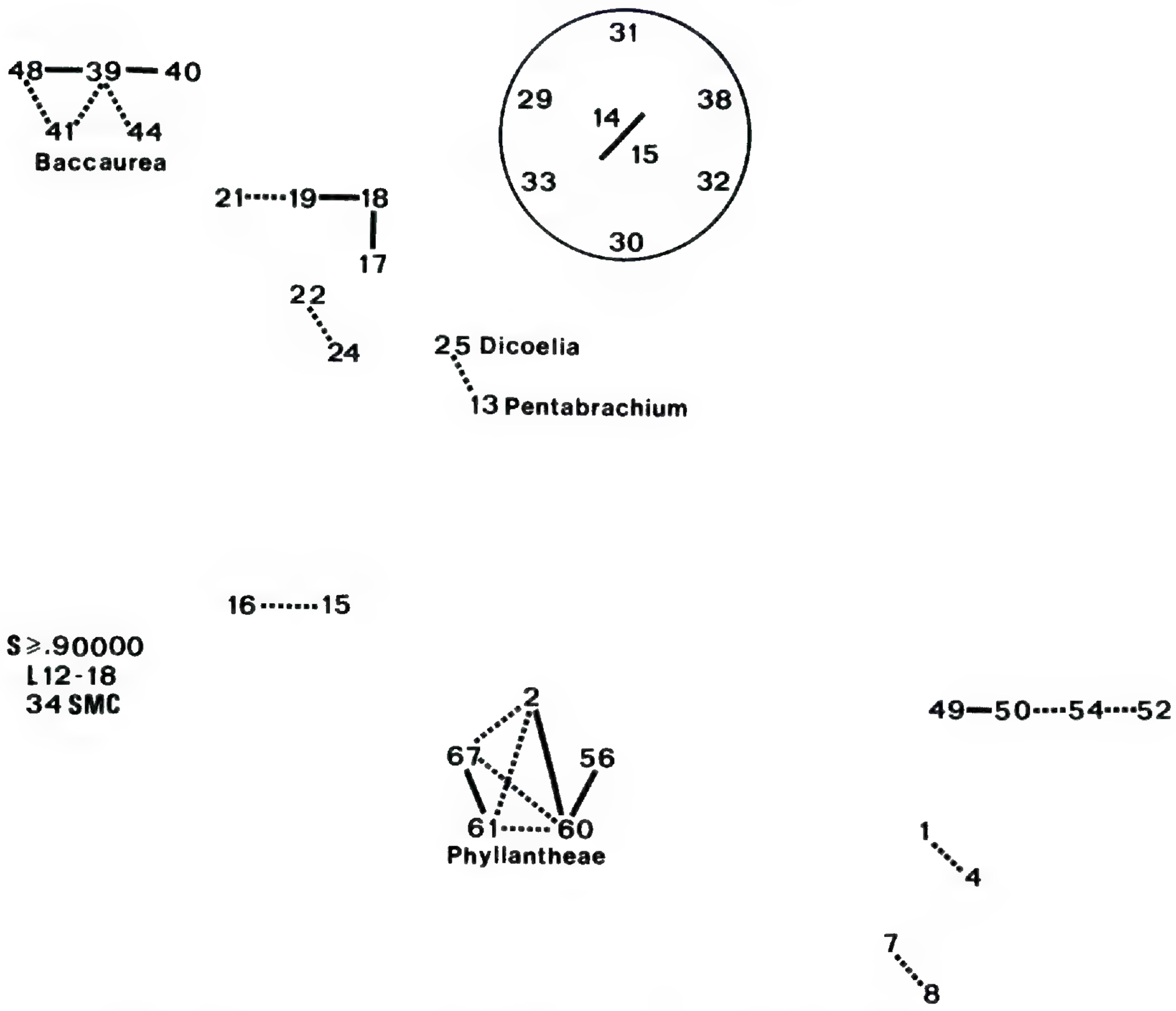

FIGURE 2. Clusters present in SIMGRA analysis at level 18 or similarity value 0.90000.

form a single cluster, with OTU 56, *Jablonskia,* connected to only one OTU of an otherwise completely interconnected cluster of members of the Phyllantheae. The clusters representing *Cleistanthus* and *Drypetes* each gain one or two new OTUs belonging to their respective genera, but each cluster remains minimally interconnected. Two sections of *Baccaurea* rather loosely join C-39. Thirty-four SMCs remain.

By similarity level 0.88222 (Fig. 3), only one new cluster forms and C-1 remains unchanged. The most marked change is the joining of C-13, C-17, C-22, and C-29 into a single cluster. CSC-29 is joined by other OTUs in the Antidesmeae, *Antidesma* sect. *Ghaesembilla* (34) and *Hyeronima* (36). C-2, C-49, and C-39 become more tightly connected internally, and the latter is joined by OTU 46, *Maesobotrya.* OTUs 6 and 9 connect to C-7, which now consists of *Savia* and its segregates *Blotia* and *Petalodiscus.* OTU 14 joins the other OTUs in *Bridelia.* Twenty-five SMCs remain.

By level 31 (Fig. 4), only 16 SMCs remain. C-1 and C-6 join by a connection between *Wielandia* (1) and *Savia* (6) to form most of the Wielandieae. No new internal connections form within C-2, but it is joined by three genera, *Heywoodia* (3), *Keayodendron* (57), and *Bischofia* (91). C-39 joins CSC-29 by a single connection between OTUs 36 and 40, and also forms connections with a section of *Baccaurea* (43), *Protomegabaria* (47), and *Uapaca* (88). In other portions of C-13, additional connections form between the subclusters, with two sections of *Cleistanthus* (22 and 24) beginning to become connected to the other sections of the genus. A connection between OTUs 11 and 12 joins the two OTUs in *Actephila*; the latter OTU had earlier connected with a section of *Andrachne* (27). *Neowawraea* (90) joins *Bridelia* (C-14), and *Putranjiva* (55) forms a single connection with its close relative *Drypetes* (C-49), whose members are becoming increasingly tightly interconnected.

Levels 32 through 37 (Fig. 5) see connections forming to seven SMCs and the coalescence of the earlier clusters into two large clusters. Connections between OTUs 1 and 55, 6 and 56, and 55 and 56 loosely join CSC-1 (Wielandieae pro parte), CSC-2 (roughly the Phyllantheae), and CSC-49 (Drypeteae). These subclusters remain

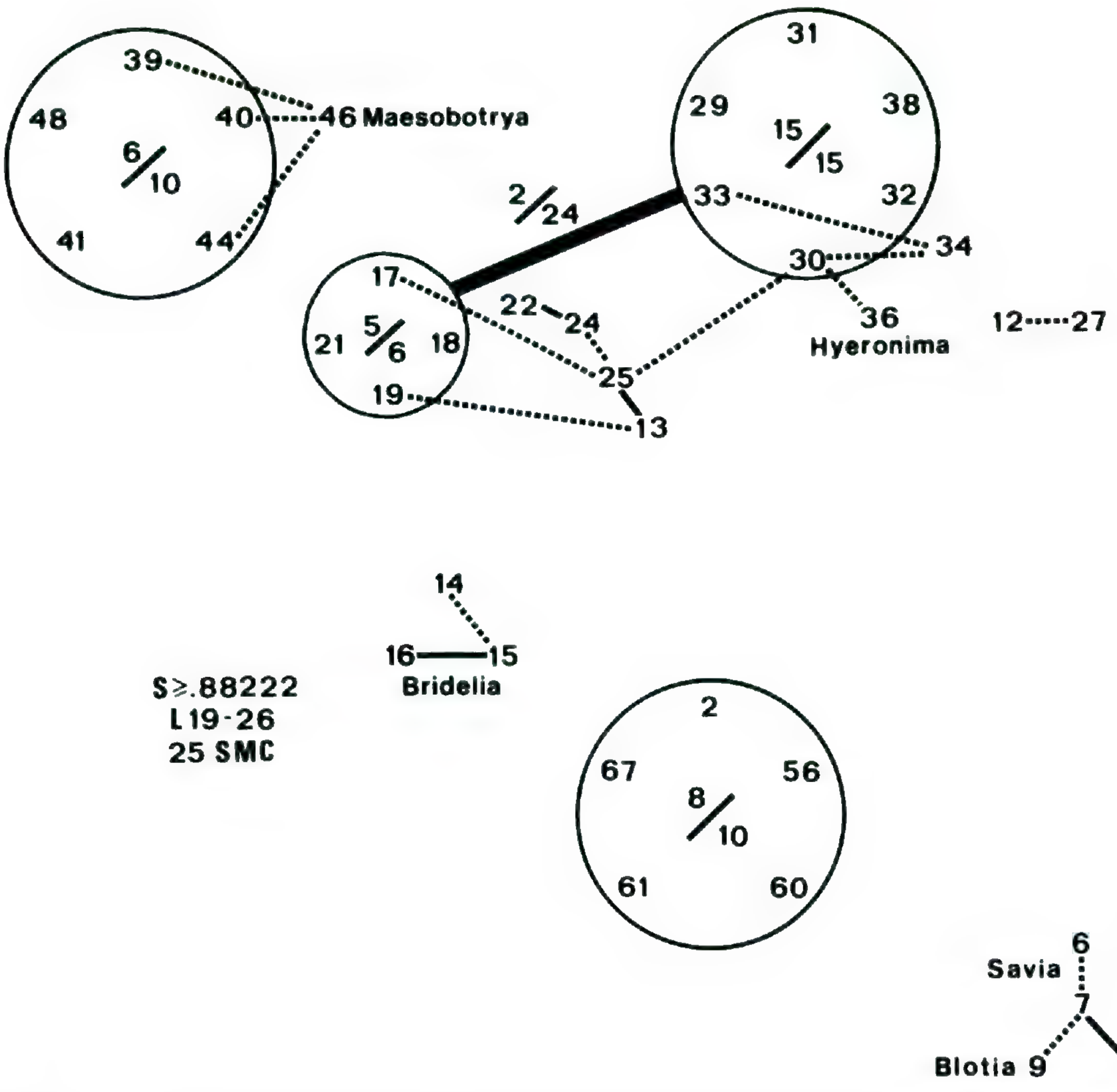

FIGURE 3. Clusters present in SIMGRA analysis at level 26 or similarity value 0.88222.

relatively unchanged at these levels: CSC-1 gains two internal connections, CSC-2 gains OTU 20, a section of *Cleistanthus,* by a connection with OTU 60, and CSC-49 gains one internal connection and another group in *Drypetes,* OTU 51. OTUs 27 and 38 connect to 26, thereby joining CSC-11 to CSC-29, the core genera of the Antidesmeae. No new connections form between CSC-13 and CSC-29, and only one between CSC-13 and CSC-17. CSC-17 gains SC-22, thus further consolidating *Cleistanthus,* and *Meineckia* (58) connects to OTU 24. *Hymenocardia* (89) simultaneously joins both *Neowawraea* (90) and OTU 18 to connect SC-14 to CSC-17. CSC-29, in addition to becoming increasingly highly internally connected, increases its association with CSC-17 through four new connections and with CSC-39 through three. CSC-39 gains only OTU 42, but increases both its internal connectedness and its connectedness to OTU 47. This subcluster now corresponds to the Aporuseae of Webster (1975), less *Didymocistus* (45), which remains among the nine SMCs.

At level 45 (Fig. 6), all OTUs belong to one cluster. This large cluster is composed of eight circular subclusters and six fairly isolated OTUs. The Wielandieae pro parte, CSC-1, in addition to becoming more tightly connected internally, gain *Discocarpus* (5) through a connection to *Petalodiscus* (8), form a new connection to CSC-11, and connect further to CSC-2 both directly and through newly added OTUs 10 (*Amanoa*) and 93 (*Croizatia*). The connection between CSC-1 and CSC-2 is the strongest between any two subclusters. CSC-2, which with the addition of *Pseudolachnostylis* (59) consists of most of the Phyllantheae, *Astrocasia* (2) and *Heywoodia* (3) of the Wielandieae, and a section of *Cleistanthus,* connects with six other subclusters, albeit generally weakly. *Amanoa* (10), *Celianella* (35), and *Croizatia* (93) all form connections with CSC-2 late in SIMGRA analysis; in fact *Amanoa* is the last OTU to join the cluster, connecting simultaneously to OTUs 1 and 56 at level 45. CSC-11 (*Actephila* and *Andrachne*), CSC-14 (*Bridelia*), and CSC-45 (*Didymocistus, Hymenocardia,* and *Neowawraea*) become very highly or completely internally connected subclusters that remain fair-

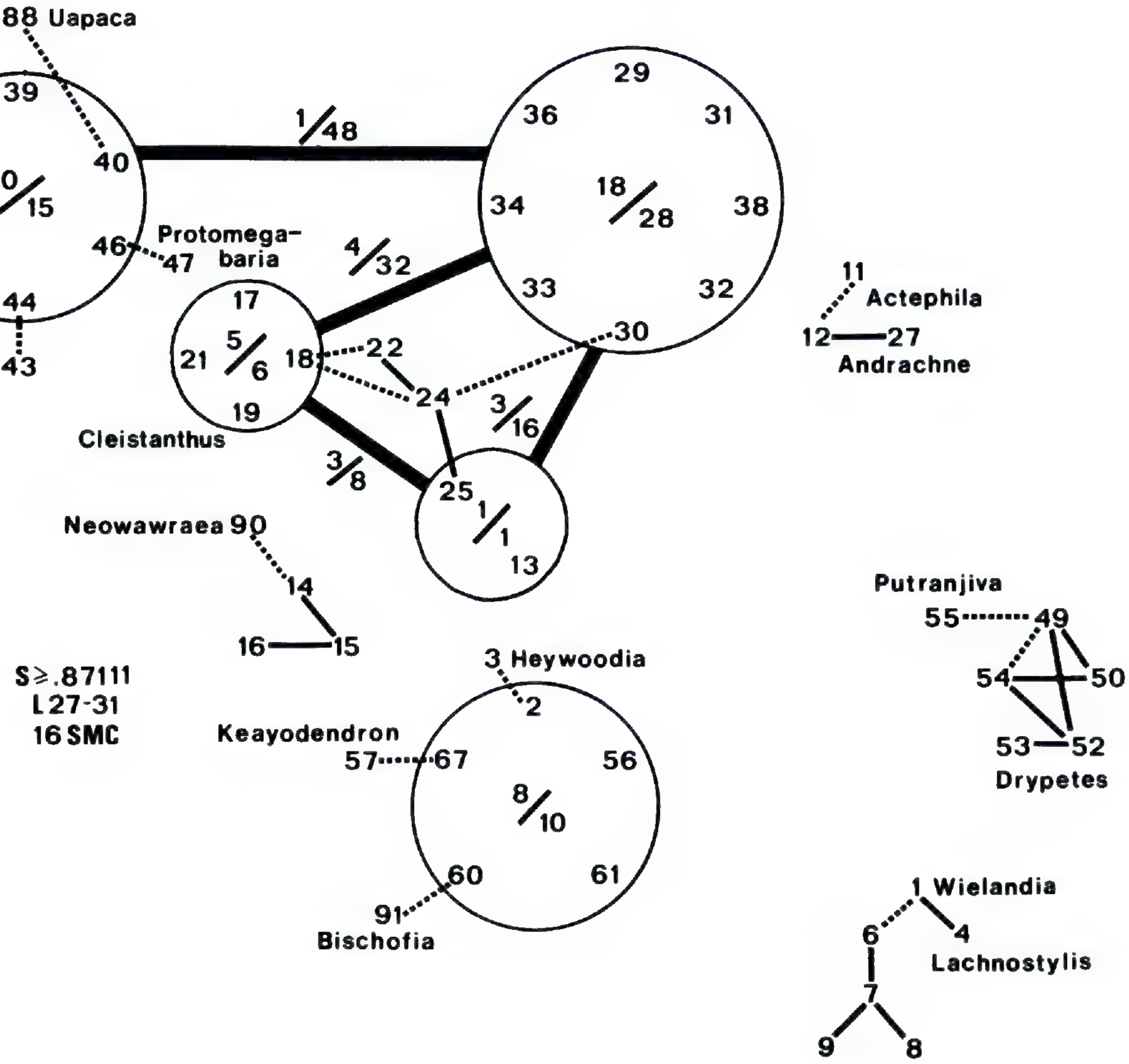

FIGURE 4. Clusters present in SIMGRA analysis at level 31 or similarity value 0.87111.

ly isolated from other subclusters. CSC-49, the Drypeteae less *Neowawraea,* is less tightly internally connected than these, but also is quite isolated. Two OTUs connect to CSC-11: a section of *Cleistanthus* (23), which connects at level 38, and *Martretia* (92), which connects at level 42. *Leptonema* (37) forms six connections to members of SC-29, which, together with CSC-17, simultaneously joins to CSC-13. CSC-13 thus consists of most of *Cleistanthus* (17–19, 21, 22, and 24), *Dicoelia* (25), *Meineckia* (58), *Pentabrachium* (13), and the Antidesmeae (29–34, 36–38) less *Celianella* (35). *Spondianthus* (28) forms six connections to SC-29. The final subcluster, CSC-39, consisting of the relatively tightly connected Aporuseae (39–44, 46–48) more loosely joined by *Uapaca* (88), connects fairly closely with CSC-13, but is otherwise comparatively isolated.

In addition to the SIMGRA analysis using both architectural and cuticular characters, I also performed an analysis using only the 26 architectural characters in order to examine their power to group the OTUs. The results were similar in both cases. Inclusion of the genera with phyllanthoid branching introduced convergence that muddled the clusters, so I again deleted them. The same major clusters formed in approximately the same order, but tended to be somewhat less tightly connected internally and to have more connections to other clusters. This was particularly true of CSC-2, which consists of genera Webster (1975) placed in the Phyllantheae and the Wielandieae. CSC-39, the Aporuseae and Uapaceae, appeared more similar to the Antidesmeae when only architectural characters rather than all the foliar characters were used. *Cleistanthus,* with *Dicoelia* and *Pentabrachium,* remained more distinct from the Antidesmeae, so that at the conclusion of the clustering, CSC-13 of Figure 6 would have been represented better by two circular subclusters. Thus the inclusion of cuticular characters generally improved the resolution of the groups but may have caused a few to appear more similar than they otherwise

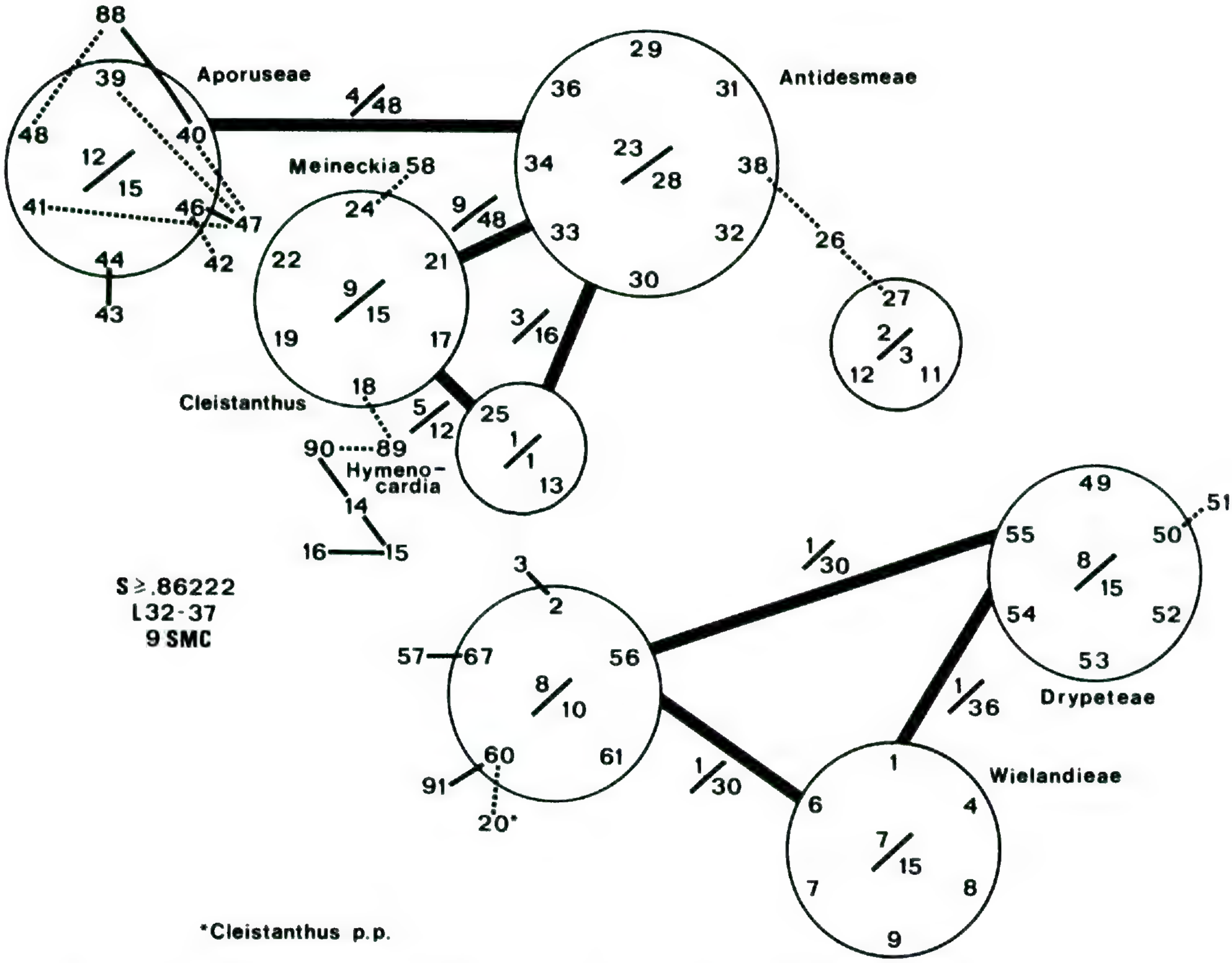

FIGURE 5. Clusters present in SIMGRA analysis at level 37 or similarity value 0.86222.

might. I attempted no analysis using only cuticular characters because too few characters were involved.

DISCUSSION

COMPARISON WITH PREVIOUS CLASSIFICATIONS

The groups that formed during SIMGRA analysis of leaf characters alone correspond remarkably well to taxa proposed by other systematists, particularly Webster (1975), whose use of different sources of systematic information was the most comprehensive. The large subclusters in Figures 5 and 6 are almost equivalent to his major tribes, notably the Antidesmeae, Aporuseae, Drypeteae, Phyllantheae, and Wielandieae. Several genera he and others have considered very isolated based on other characters, e.g., *Bischofia, Hymenocardia, Martretia,* and *Spondianthus,* connect late in the analysis, corroborating their distinctiveness. Furthermore, putative relationships between taxa are frequently reflected by the degree of connectedness between the corresponding subclusters, as in the cases of the comparatively close associations between the Antidesmeae and the Aporuseae, *Spondianthus* and the Antidesmeae, and between the Phyllantheae and the Wielandieae, and the relatively isolated position of the Drypeteae.

A one-to-one correspondence does not exist between the SIMGRA results and any previous classification, however, and there are several notable discrepancies. One of the most obvious of these involves the genus *Cleistanthus,* which I divided into eight OTUs that approximate sections (OTUs 17–24). Of these, four became very highly connected by level 31 (Fig. 4; CSC-17), and two more joined the subcluster soon thereafter (Fig. 5). The two remaining OTUs, sects. *Chartacei* (20) and *Australes* (23), remained SMCs until late in the analysis, and even then did not form connections with the *Cleistanthus* subcluster. *Chartacei* formed connections with eight OTUs, five of which are in CSC-2 and none of

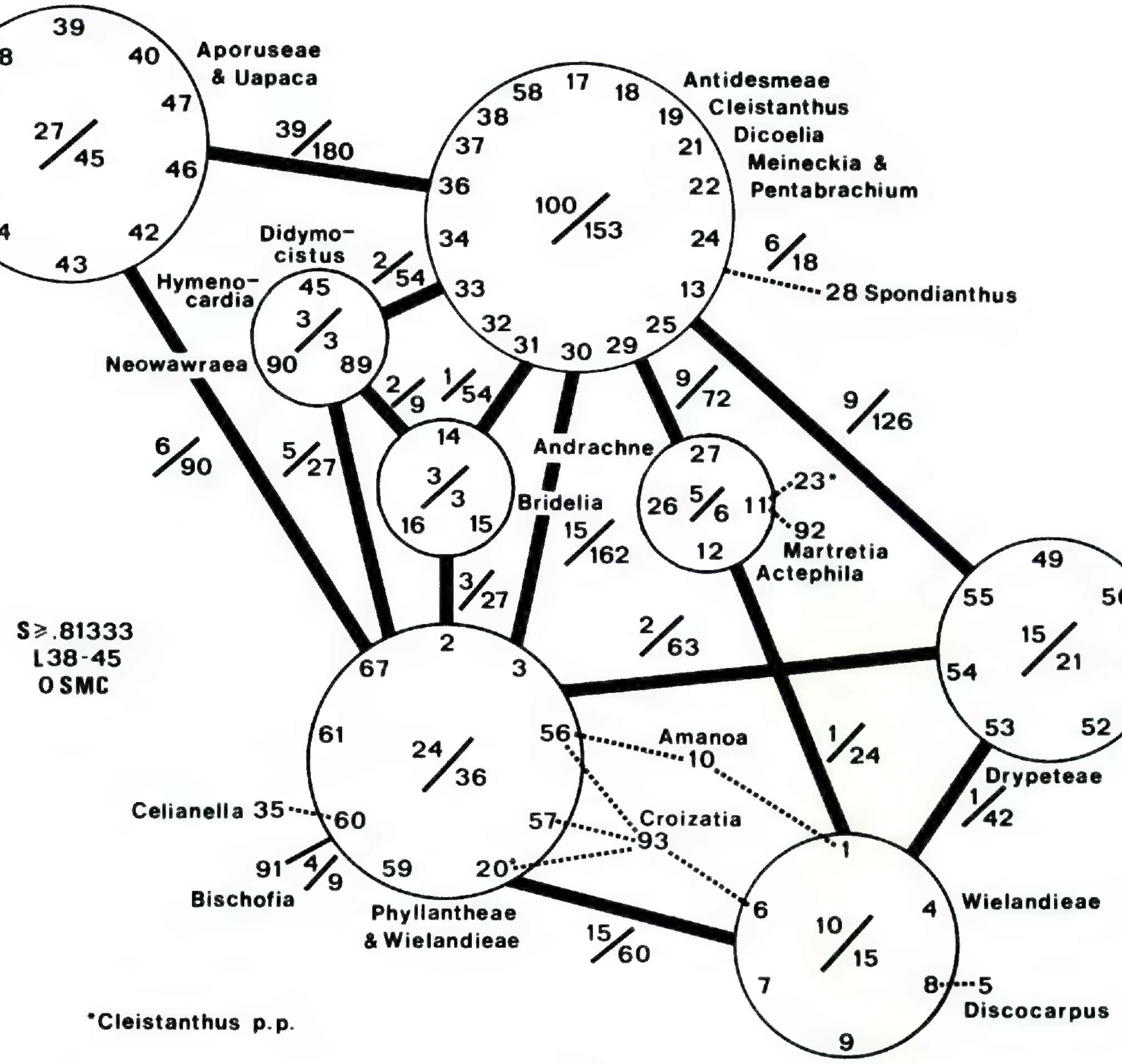

FIGURE 6. Clusters present in SIMGRA analysis at level 45 or similarity value 0.81333.

which are in *Cleistanthus*. *Australes* are even more distant, forming a single connection to *Actephila* at level 38. Jablonsky (1915) felt that *Australes*, although clearly in *Cleistanthus*, are rather isolated within the genus and also noted that the leaves of *C. cunninghamii*, the only species in *Chartacei* I examined, are not typical of the section. Apparently leaves of these two taxa exhibit sufficient non-divergent change that overall similarity poorly reflects relationship.

In most systems *Cleistanthus* and *Bridelia* (14–16) are considered to be closely related because they have very similar flowers with valvate sepals (Jablonsky, 1915) and similar pollen (Punt, 1962; Köhler, 1965). Webster (1975), on the basis of the pollen evidence, placed the two genera in their own tribe near the Wielandieae. Phenetic analysis of the foliar characters considerably separates the two genera. Most members of *Cleistanthus* were closely allied with *Dicoelia* and the Antidesmeae, whereas *Bridelia* remained fairly isolated and formed only a single connection with *Cleistanthus* at the final level of similarity. *Bridelia* leaves are extremely specialized within the Phyllanthoideae (Levin, 1986), and therefore appear isolated in a phenetic analysis. Cladistic analysis, which de-emphasizes the unique character states (autapomorphies) of *Bridelia*, supports the relationship between the genera (Levin, in press).

Another difference from the classifications of Webster and others lies in the assignment of genera to the Wielandieae and the Phyllantheae. In particular, leaves of *Astrocasia* (2) and *Heywoodia* (3), genera usually included in the Wielandieae, are more similar to leaves of the Phyllantheae. Webster (1956) had previously suggested a relationship between *Astrocasia* and the Phyllantheae, and both Punt (1962) and Köhler (1965) remarked on the close resemblance

among the pollen of these taxa. Pollen and other reproductive structures of *Heywoodia* are less similar to the Phyllantheae. The main reason for retaining *Astrocasia* and, to a lesser extent, *Heywoodia* in the Wielandieae is their petaliferous flowers, a characteristic that, because it is primitive in the subfamily (Webster, 1967), might not necessarily be expected to reflect phylogenetic relationships. Cladistic analysis of the foliar characters in fact clearly associates *Astrocasia* with the Phyllantheae but retains *Heywoodia* in the Wielandieae (Levin, in press).

Meineckia (58), placed in the Phyllantheae by Webster (1965, 1975), connected with the bulk of *Cleistanthus* late in the SIMGRA analysis (Figs. 5, 6). Associated with the herbaceous tendencies of *Meineckia* is a reduction in the organization of its leaves (Levin, 1986), which obscures its relationships. A similar phenomenon probably explains the unexpected connection at level 43 between *Celianella* (35), a member of the Antidesmeae (Jablonsky, 1965; Webster, 1975), and *Zimmermannia* (60) of the Phyllantheae (Fig. 6). The leaves of *Celianella* are quite thick and have unusual reduced venation (Levin, 1986). In both of these cases, cladistic analysis of leaf characters yields results that are much closer to the classifications of Webster (1975) and others (Levin, in press).

Another difference between the SIMGRA results and Webster's (1975) classification involves the treatment of *Amanoa* (10), *Actephila* (11,12), and *Croizatia* (93), which Webster included in their own tribe, the Amanoeae. At similarity level 45, the final level shown in the SIMGRA analysis (Fig. 6), *Amanoa* simultaneously formed connections with *Wielandia* (1) and *Jablonskia* (56), and at only slightly lower similarity levels additional connections would form between *Amanoa* and other OTUs in CSC-1, containing genera in the Wielandieae, but not with either *Actephila* or *Croizatia*. Thus *Amanoa* appears most closely related to the Wielandieae, a relationship also suggested by pollen morphology (Punt, 1962; Köhler, 1965).

The leaves of *Actephila* (11, 12), in contrast, more closely resemble those of *Andrachne* (26, 27). The two genera first connected at level 24 (Fig. 3), and, by the end of SIMGRA analysis, they formed a tightly connected and rather isolated subcluster (Fig. 6). Both Punt (1962) and Köhler (1965) emphasized the similarity between the pollen of *Andrachne* and *Actephila*. Again, although SIMGRA analysis of the foliar morphology contradicts previous classifications, the concordance with pollen implies that leaf results may better reflect actual relationships.

Croizatia (93) has similar fruits to *Actephila* (Steyermark, 1952) but has very different leaves (cf. Fig. 6). Until *Croizatia* is better known, its relationships will remain uncertain.

In addition to its implications regarding the relationships of *Actephila,* the constitution of CSC-11 is significant also in that *Andrachne* sect. *Phyllanthopsis* (27) has been placed in *Savia* (6 and 7; CSC-1) by many authors (e.g., Pax & Hoffman, 1922), although palynology (Punt, 1962; Köhler, 1965) and some aspects of floral morphology (Webster, 1967) suggest that this section is in fact better placed in *Andrachne,* in accord with the leaves. The most striking feature uniting the leaves of different *Andrachne* sections is their anisocytic stomata, which is a derived condition in the Phyllanthoideae (Levin, in press).

Previously unsuspected on other evidence is the relationship suggested by foliar morphology between *Uapaca* (88) and the Aporuseae (CSC-39, Fig. 6). As I discussed previously (Levin, 1985), floral morphology, palynology, and wood anatomy, which have been the principal sources of taxonomic information in the Phyllanthoideae, have little to offer toward clarifying the relationships of *Uapaca* because it has so many unique specializations. However, in SIMGRA analysis, as in cladistic analysis (Levin, in press), both the totality of foliar characters and architectural characters alone consistently associate *Uapaca* with the Aporuseae. These foliar results suggest that the other organs of the genus be reexamined with this possible relationship in mind.

Equally novel is the suggestion (Fig. 6, CSC-45) of relationships between *Didymocistus* (45), *Hymenocardia* (89), and *Neowawraea* (90). Webster (1975), following other authors, placed these genera in three different tribes: the Aporuseae, the monotypic Hymenocardieae, and the Drypeteae, respectively. Both *Didymocistus* and *Neowawraea* have leaves that would be quite anomalous in the tribes to which Webster referred them (Levin, 1986). The high degree of organization of the venation makes all three genera quite similar to each other and to the Phyllantheae, as does wood anatomy (Metcalfe & Chalk, 1950; Hayden & Brandt, 1984; Mennega, 1984). The palynological literature has little to offer, because *Hymenocardia* has very unique pollen and the other two genera have not been examined.

Finally, Webster (1975) excluded *Martretia* (92) from the Phyllanthoideae, and indeed from the Euphorbiaceae altogether, although previous authors had placed it in the Antidesmeae. Its fruit and pollen characters are indeed unique in the family (Levin, 1986), and because it is one of the last OTUs to join a cluster in SIMGRA analysis, Webster may have been correct to remove *Martretia* from the Phyllanthoideae, if not also from the family.

POTENTIAL FOR USE IN IDENTIFICATION

Both Dolph (1976) and Hill (1980) had as their primary goal identification of fossil leaves, not classification of an extant group. Both found that phenetic analysis of their character sets generally associated different leaves of the same species but led to the recognition of no higher taxa. Their character sets tend to emphasize aspects of size and shape, most of which I found to be relatively invariable at the species level within the Phyllanthoideae, but highly variable within genera and higher taxa (Levin, 1986). However, given an unknown leaf from a member of the Phyllanthoideae, the characters I used would probably associate it with the correct genus or higher taxon.

Two problems arise using these characters for the identification of fossil leaves. The first is the obvious one: How do we know whether a particular fossil leaf belongs to the Phyllanthoideae? As I discussed in another paper (Levin, 1985), characters that neither Dolph, nor Hill, nor I included in our character sets may help narrow the choice of higher taxa. An example of such a character is the type of marginal toothing that Hickey and Wolfe (1975) found to be quite characteristic of families and higher taxa. Dolph (1976) and Hill (1980) excluded tooth type from their character sets to avoid statistically weighting the analysis in favor of toothed leaves at the expense of entire-margined leaves. I did not include tooth type in my study because it is invariable within the Phyllanthoideae; for the same reason I did not include other characters, e.g., pinnate versus palmate venation, that may help separate the leaves of the Phyllanthoideae from those of other taxa. Thus the placement of leaves in higher taxa requires not phenetic analysis using equally weighted characters, but the recognition of diagnostic characters that delimit large groups. Hill (1980) noted the same problem. Clearly, detailed examination of many more extant groups, coupled with cladistic analysis to identify diagnostic characters in those groups like the Phyllanthoideae that have relatively nondescript leaves, will be necessary before we can accurately relate many fossil leaves to leaves of their extant relatives.

The way SIMGRA analysis handled *Martretia* offers some indication of the way in which phenetic analysis might treat taxa not initially assigned to the correct higher taxon. Because of its substantial differences from other members of the Phyllanthoideae (although more in the combination of character states than in any particular character), *Martretia* joined late in the analysis. However, it still connected earlier than such aberrant but bona fide Phyllanthoideae as *Amanoa, Didymocistus, Discocarpus, Leptonema,* and *Spondianthus.*

The second problem, which was extensively addressed by both Dolph (1976) and Hill (1980), involves missing data. Many fossil floras include leaves that lack well-preserved higher order venation and/or cuticle. That the SIMGRA analysis of architectural characters alone yielded clusters that were less well resolved but substantially similar to clusters that formed using the entire character set suggests that cuticle may not always be essential to proper identification. However, as the preservation of venation becomes poorer, the confidence of identification could be expected to decrease considerably.

CONCLUSIONS

Phenetic analysis using leaf architectural and cuticular characters in the Phyllanthoideae produces groups similar to those in classifications based on characters more widely recognized as being of systematic value, such as floral morphology, palynology, and wood anatomy. Most exceptions appear not to be cases in which the leaf evidence is spurious, but in which there is also evidence from some other fields that the classifications are invalid. A similar but less well resolved clustering results from analysis of architectural characters alone. That numerical analysis yields such clear results in a group not known for having diagnostic leaves argues against the widely held idea that angiosperm leaves are so evolutionary and environmentally plastic that they are of little systematic value. At least in the Phyllanthoideae, the amount of parallelism and convergence in leaf architectural and cuticular characters is small enough that overall similarity

usually reflects presumed evolutionary relationship.

In a few cases, for example *Meineckia, Celianella,* some sections of *Cleistanthus,* and the phyllanthoid-branching genera in the Flueggeinae, excessive convergence does cloud relationship. In these cases, I feel that it is not so much a fault of the characters as it is the inherent weakness of systematic methods based on total similarity. The results of cladistic analysis of the same data even more closely resemble previous classifications (Levin, in press). The greater ability of cladistic methods to discriminate between divergent and non-divergent evolutionary change, and to factor out autapomorphies, minimizes the effects of these problems.

Because this is the first report of numerical analysis of the foliar morphology of a related group of flowering plants, the need for more studies remains. The characters employed were derived from systems developed for the description of fossil and modern angiosperms (Stace, 1965; Hickey, 1973) and are therefore widely applicable. Further examination and analysis of extant angiosperms should help us to understand better the patterns of leaf evolution in the flowering plants and to classify more confidently the leaves of fossil plants.

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NOTES ON THE FLORAL BIOLOGY OF *COUROUPITA GUIANENSIS* AUBL. (LECYTHIDACEAE)[1]

SONIA YARSICK, NERIDA XENA DE ENRECH, NELSON RAMIREZ, AND GETULIO AGOSTINI[2]

Floral biology has been studied in relatively few Lecythidaceae, despite their ecological importance in the Neotropics. Only a few authors have dealt with the subject, notably Jackson and Salas (1965) on *Lecythis ellipitica* H.B.K., Dias (1967) on *Bertholletia excelsa* Humb. & Bonpl., Mori and Kallunki (1976) on *Gustavia superba* (Kunth) Berg., Prance (1983) on *Eschweilera garagarae* Pittier, and Prance (1976) and Mori et al. (1978) on pollination and androecial structure in the family as a whole. Ormond et al. (1981) published a contribution to the floral biology of *Couroupita guianensis* after all of our field observations were completed and a draft of this paper was submitted for publication. Prance (1976) and Mori et al. (1978) pointed out that the androecial zygomorphy and the position of the hood (adpressed to the ring) in *Couroupita subsessilis* Pilg. suggest that the genus *Couroupita* may be intermediate in the family with respect to androecial evolution. Few studies of anthesis behavior in tropical plants, including Lecythidaceae, have been carried out. Notably, Mori et al. (1978) reported diurnal anthesis and shedding of stamens during the late afternoon for *Lecythis amara* Aublet (= *L. alba* Mori, nom. nud.), and asynchronous anthesis during the morning for *Eschweilera longipes* (Poit.) Miers.; the latter of which sheds its androecia the following day. Differential behavior between pollen produced in ring anthers and that found in hood anthers is documented by Mori and Orchard (1979), Mori et al. (1980a), and Ormond et al. (1981). Floral visits by potential pollinators, such as wasps and small bees, have been reported by Prance (1976), Mori et al. (1978), and Ormond et al. (1981).

METHODS AND RESULTS

Cultivated individuals of *Couroupita guianensis* Aubl. were studied at the Jardin Botanico in Caracas, Venezuela, located near the limit of natural distribution of the species. Observations were recorded during two days in November 1979, and again for four days in June 1980, although the observed individuals flower throughout the year.

The flowers of *Couroupita guianensis* are very fragrant and attract many insect visitors. The petals are yellow both on the exterior and the interior, with rose to red-rose margins. The androecial column and filaments of the hood stamens are lilac, with the tip of the anthers yellow and the ring stamens white. A small amount of sticky secretion is present on the stigma. Anthesis is diurnal and asynchronic, the flowers beginning to open gradually between 7:00 and 8:30 A.M., with a peak around 8:00 A.M. (Fig. 1). The ring anthers open simultaneously with those on the hood, shortly after anthesis, but they retain pollen longer during the day (Fig. 2). The number of open flowers presenting pollen reaches a peak around 9:00 A.M.

Pollen in *Couroupita* is dimorphic; grains produced by anthers in the hood are released in tetrads and as such are clearly larger than the simple grains produced in the ring anthers. Furthermore, the hood anthers themselves are larger, containing an average of 2,850 tetrads, as compared with approximately 450 grains per ring anther. Tests for pollen viability show no germination of hood pollen in sacharose, as previously reported by Mori et al. (1980b) and by Ormond et al. (1981). However, Thompson (1921) reported that hood pollen was as fertile as ring pollen. Hood pollen stained well using cotton blue in lactophenol and it is reported by Ormond et al. (1981) as having significant protoplasm in 88% of pollen grains tested using aceto carmine. These reports raise doubts as to the reliability of both staining methods for assessing pollen viability.

[1] We appreciate the use of facilities at the Jardin Botanico and Instituto Botanico (MARNR) in Caracas. We wish to mention the valuable collaboration of the 1980 course in Biosystematics and the help of Mr. L. Diaz (Technician), Mr. Sixto Garcia (Artist), and Lic. Celia Gil. We thank Drs. S. Mori and G. T. Prance of the New York Botanical Garden, and Stephen S. Tillett of the Herbario V. M. Ovalles, Facultad de Farmacia, Universidad Central de Venezuela, for reading and correcting the original manuscript.

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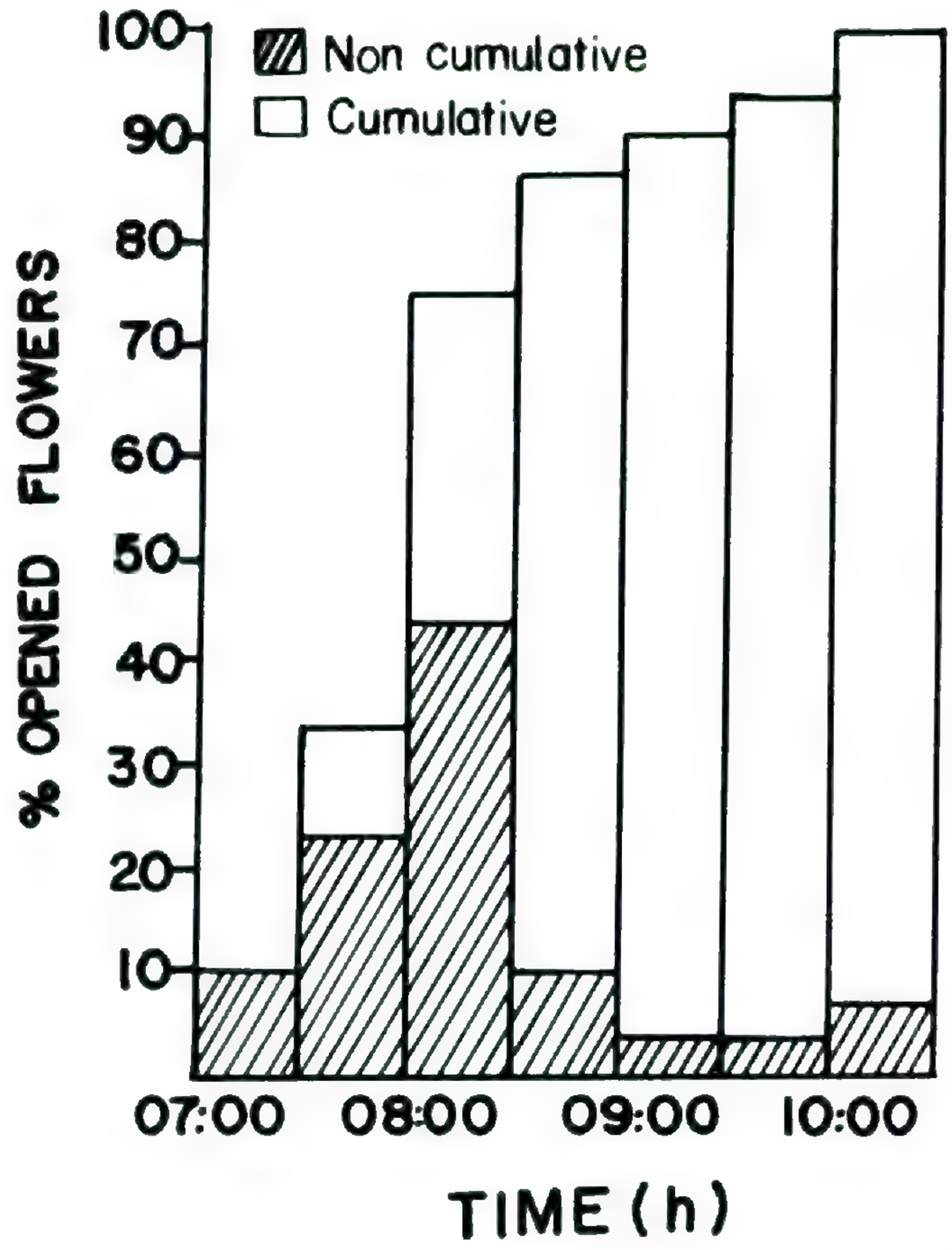

FIGURE 1. Anthesis behavior in *Couroupita guianensis*.

Insects captured visiting flowers were bees belonging to *Apis mellifera, Bombus* sp., *Trygona* sp., and *Xylocopa frontalis* (Oliver), the wasp *Polybia,* and the flower fly *Ornidia obesa* F. (Diptera, Syrphidae). More frequent visits were made by the larger insects, such as individuals of the bee genera *Bombus* and *Xylocopa,* which have been reported as visitors to Lecythidaceae, including species of *Gustavia, Eschweilera, Couratari,* and *Couroupita guianensis.* Less frequent visits were made by the smaller insects, such as

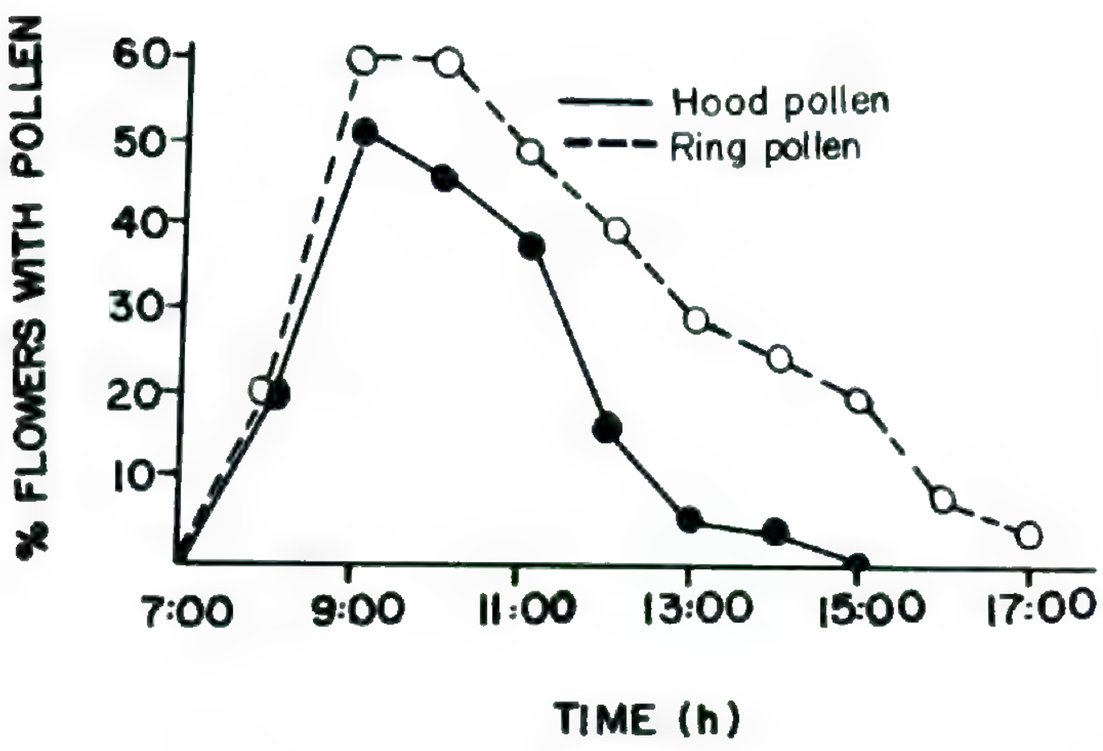

FIGURE 2. Comparison of behavior of anther dehiscence and pollen extinction between the hood and the ring in flowers of *Couroupita guianensis.*

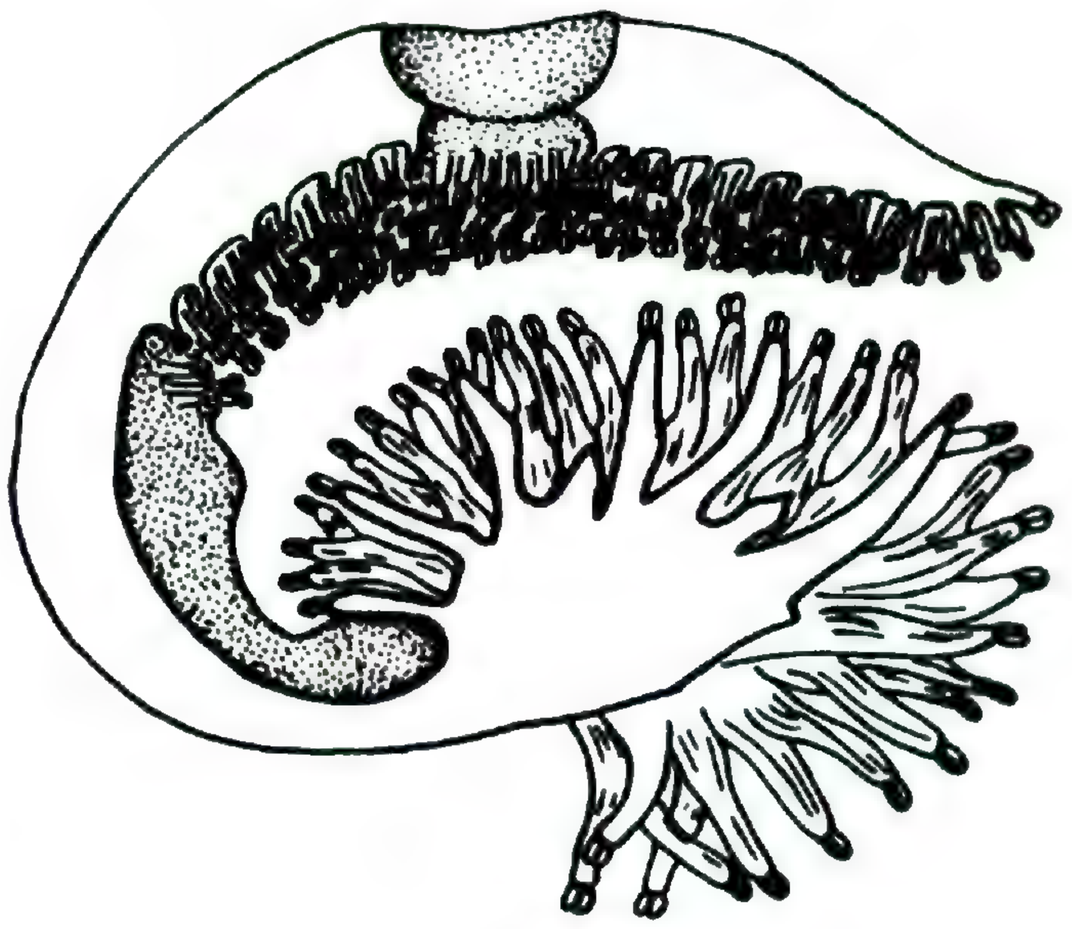

FIGURE 3. Medial schematic section of androecium in *Couroupita guianensis.*

species of *Apis, Trigona,* and the wasp genus *Polybia,* which have been observed in numerous Lecythidaceae, including *Couroupita subsessilis,* a species which has much smaller flowers (Prance, 1976). Thus, *Couroupita guianensis* differs from *C. subsessilis,* as well as other Lecythidaceae, in atracting both small and larger insects, including species of the mentioned genera.

The hood anthers of *C. guianensis* provide a convenient landing platform for these floral visitors, because the flowers are inverted and hanging (Fig. 3). The open structure of the androecium facilitates access to insects of various sizes. While collecting hood pollen, larger bees rub their dorsal areas against the ring anthers and the stigma, detaching several ring anthers in the process. This behavior assures transfer of ring pollen to the stigma. Apparently hood pollen may also reach the stigma, however, because insects were observed to turn over completely within the flower. Individuals of *Trigona* forage for pollen

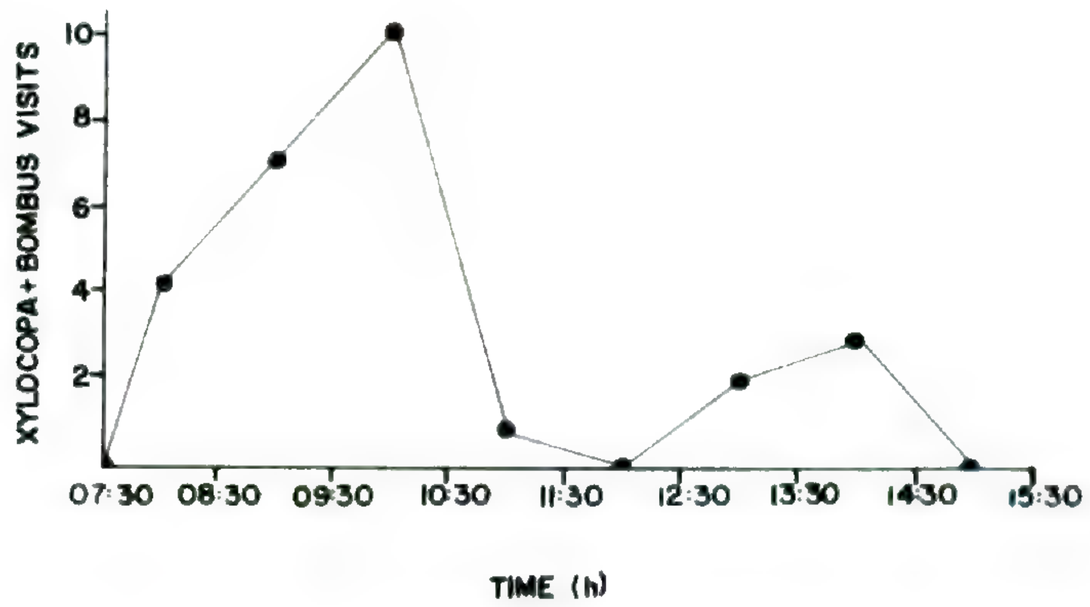

FIGURE 4. *Bombus* and *Xilocopa* visits recorded, as an average of five days, in flowers of *Couroupita guianensis.*

on ring anthers during long periods, probably affecting pollination, whereas other small floral visitors wander throughout the flower in such a manner that only their ventral surfaces contact the anthers, and pollination thus occurs only accidentally.

Data on frequency of floral visits by individuals of *Bombus* sp. and *Xylocopa frontalis* were recorded (Fig. 4). Visits began at anthesis and continued throughout the day, with peaks occurring around 10:00 A.M. and 2:00 P.M., and a drop to near zero and around noon. *Bombus* species tended to visit predominantly in the morning, while *Xylocopa* were more common in the early afternoon.

Discussion

Our findings on pollen fertility and pollen behavior confirm that pollination is achieved only with ring pollen. However, hood pollen, which should be rich in nutrients, as suggested by its living protoplasm, provides only food for the pollinators, and plays an important role in the process of pollination, as was previously stated by Ormond et al. (1981).

Our observations for *Couroupita guianensis* as compared to reported data for *C. subsessilis* (Prance, 1976) suggest that differential use of pollinators may be important in the evolution and maintenance of species within the genus. It is interesting to note that individuals of *Bombus* and *Xylocopa* have been seen on putatively primitive Lecythidaceae such as *Gustavia,* as well as on more advanced taxa such as species of *Couratari.* It is therefore not surprising to find these larger floral visitors on *Couroupita,* whose androecial structure is apparently intermediate within the family.

The asynchronous behavior of anthesis observed in *C. guianensis* may tend to compensate for the short life of the flowers of this species and could be viewed as a way to promote cross pollination by means of prolonging pollen presentation for a period of nearly two hours. This hypothesis is supported by the distribution of visits by insects: most visits were recorded during morning hours, at a time when a maximum number of anthers is open.

The recorded frequency of floral visits, which shows that *Bombus* species tend to visit predominantly in the morning whereas *Xylocopa* were more common in the early afternoon, may document a case of temporal resource partitioning by the insects to reduce competition for pollen.

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CONVERGENT EVOLUTION OF THE '*HOMERIA*' FLOWER TYPE IN SIX NEW SPECIES OF *MORAEA* (IRIDACEAE–IRIDEAE) IN SOUTHERN AFRICA[1]

PETER GOLDBLATT[2]

ABSTRACT

Six new species of *Moraea*, all with similar small, pale to deep blue-purple flowers and reduced style branches instead of the broad petaloid style branches typical of the genus, are described from the southwest and interior west coast of southern Africa. This flower type, typical of the southern African *Homeria*, was previously known only in a few species of *Moraea*, notably sect. *Polyanthes*, and the flowers of the new species resemble especially those of *M. crispa*. However, of the new species only *M. pseudospicata* appears related to *M. crispa*. The others differ either in vegetative morphology, chromosome number, or in details of the flower, and the unusual flower seems to have evolved independently in at least three of them. *Moraea graniticola*, *M. hexaglottis*, and *M. rigidifolia* are each known from single populations in the southern Namib Desert of Namibia and are referred to sect. *Moraea*. *Moraea worcesterensis*, known from one site near Worcester in the southwest Cape, is probably closely related to *M. algoensis* of sect. *Vieusseuxia*. *Moraea deserticola*, restricted to the Knersvlakte in southern Namaqualand, is allied to *M. speciosa* of sect. *Polyanthes*.

Moraea is a widespread African genus of some 115 species of seasonal, corm-bearing perennials of the Old World tribe Irideae of the large and nearly worldwide subfamily Iridoideae. It is the major genus of subtribe Homeriinae, an alliance centered in southern Africa but extending through tropical Africa into the Mediterranean and Middle East. The alliance is characterized by having an astelic corm of a single internode and distinctive, secondarily bifacial leaves (equitant isobilateral leaves are basic in Iridaceae). *Moraea* is the largest of the eight currently recognized genera of the subtribe and occurs almost throughout sub-Saharan Africa, but species are concentrated in highland areas of southeast tropical and southern Africa and in the winter rainfall area of southern Africa. It is relatively well known taxonomically, having been revised recently (Goldblatt, 1973, 1976b, 1977). Despite intensive study, new taxa continue to be discovered, mainly in the winter rainfall areas of South Africa and recently in southern Namibia. Some of these were described in 1982 together with a synopsis of the genus in which 105 species in five subgenera and 12 sections were recognized (Goldblatt, 1982).

Several new species have been discovered since 1982, notably along the arid west coast and interior of southern Africa. The low and variable rainfall of the region is insufficient for species to flower every year, and this combined with the rugged landscape and general inaccessibility leaves this area relatively poorly known botanically. Six new species are described in this paper. *Moraea graniticola*, *M. hexaglottis*, and *M. rigidifolia* are each known from single populations in the southern Namib Desert of Namibia and are referred to sect. *Moraea*. *Moraea worcesterensis*, known from one site near Worcester in the southwest Cape, is probably closely related to *M. algoensis* of sect. *Vieusseuxia*. *Moraea deserticola*, restricted to the Knersvlakte in southern Namaqualand, is allied to *M. speciosa* of sect. *Polyanthes*, while *M. pseudospicata*, from the Nieuwoudtville escarpment, is closely related to the widespread Karoo species, *M. crispa*, also sect. *Polyanthos*.

All six share an unusual feature, a type of flower characteristic of the related genus *Homeria* (Goldblatt, 1980, 1981b) in which the style arms are narrow and inconspicuous and the tepals are similar in color, shape, and disposition. The

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flowers of the new species are similar also in being blue-purple, and, at least in four of them, small and extremely fugacious, opening in the late afternoon and fading at or shortly after dusk. This type of flower was previously known in a few taxonomically isolated species of *Moraea*. Despite their similarities, the flower types probably evolved independently in at least three of them. The adaptive significance of this flower is discussed after an outline of the morphology of the *Moraea* and *Homeria* flower and a review of the new species.

The description of the three new species from Namibia more than doubles the number of *Moraea* species recorded in this country from the two admitted by Sölch (1969), *M. polystachya* and *M. namibensis* (treated as *M. edulis* by Sölch). *Moraea carsonii* has also now been found in the northeast of Namibia bringing the total species of *Moraea* recorded there to six, of which three are endemic. There is in addition at least one and possibly two more known new species of the genus in Namibia, both from the extreme south of the country, at present awaiting description when adequate type material can be assembled.

Materials and Methods

CYTOLOGY

The chromosomes of five of the six new species were studied. Live material of *Moraea deserticola* was not available. Methods used are the same as those employed in similar studies in Iridaceae (Goldblatt, 1979, 1980). Root tips of sprouting corms were routinely harvested in mid-morning, pre-treated in 0.002 M hydroxyquinoline for seven to eight hours, then fixed in 3:1 absolute ethanol:glacial acetic acid for a few minutes and stored in 70% ethanol. They were hydrolyzed for six minutes in 10% HCl warmed to 60°C, then rinsed in water and squashed in FLP orcein (Jackson, 1975).

TAXONOMY

Live material of all species except *Moraea deserticola* was examined carefully, and the illustrations were made from living plants. Only cultivated plants of *M. graniticola* and *M. hexaglottis* were seen. Herbarium material from important southern African collections was also examined. Measurements were made from live plants except for *M. deserticola*. Delicate parts of the flowers probably shrink some 10–15% and the measurements for *M. deserticola* apply only to dry plants. Flower color fades progressively in dry specimens, eventually changing completely, sometimes becoming darker and usually disappearing. Color notes on collected specimens are desirable and are frequently mentioned by collectors.

Although only two sheets each of *M. graniticola, M. hexaglottis,* and *M. deserticola* were available, it seems better to describe these species now because they are relatively rare and flower irregularly, so the chance of obtaining more material is small. Also describing these species now is likely to stimulate further plant exploration in the dry interior Namib Desert where *M. graniticola* and *M. hexaglottis* occur.

Material examined is cited according to the grid reference system based on geographical degree coordinates of latitude and longitude in current use in southern Africa (Edwards & Leistner, 1971).

Cytology

The three Namib Desert species have $2n = 20$ and a similar karyotype (Fig. 1) with four long acrocentric chromosome pairs, one of which has a small satellite on the distal end of the short arm, and six much smaller submetacentric to metacentric pairs. This matches closely karyotypes found in sect. *Moraea* and is believed to be basic (Goldblatt, 1971, 1976a). *Moraea pseudospicata* and *M. worcesterensis* have $2n = 12$.

The karyotype of *Moraea pseudospicata* corresponds well to those of other members of sect. *Polyanthes* in consisting of relatively large acrocentric to submetacentric chromosomes (Fig. 1D, E). Satellites are evident on the distal arms of a long and a short acrocentric chromosome pair. Satellites have been recorded in this position in some populations of *M. crispa* and also on the end of the long arm of a long chromosome pair (Goldblatt, 1980; Fig. 1F) and in *M. polyanthos* of this section. The satellite position in other species of the section such as *M. bipartita* corresponds with that of *M. pseudospicata*.

Moraea worcesterensis has a long and a short pair of metacentric chromosomes and a long pair of strongly acrocentric chromosomes with a small satellite at the end of the short arm (Fig. 1F). This karyotype is typical of many species of sect. *Vieusseuxia* (Goldblatt, 1976a, and in prep.), and the karyotype morphology thus accords well with the placement of this species in sect. *Vieusseuxia*.

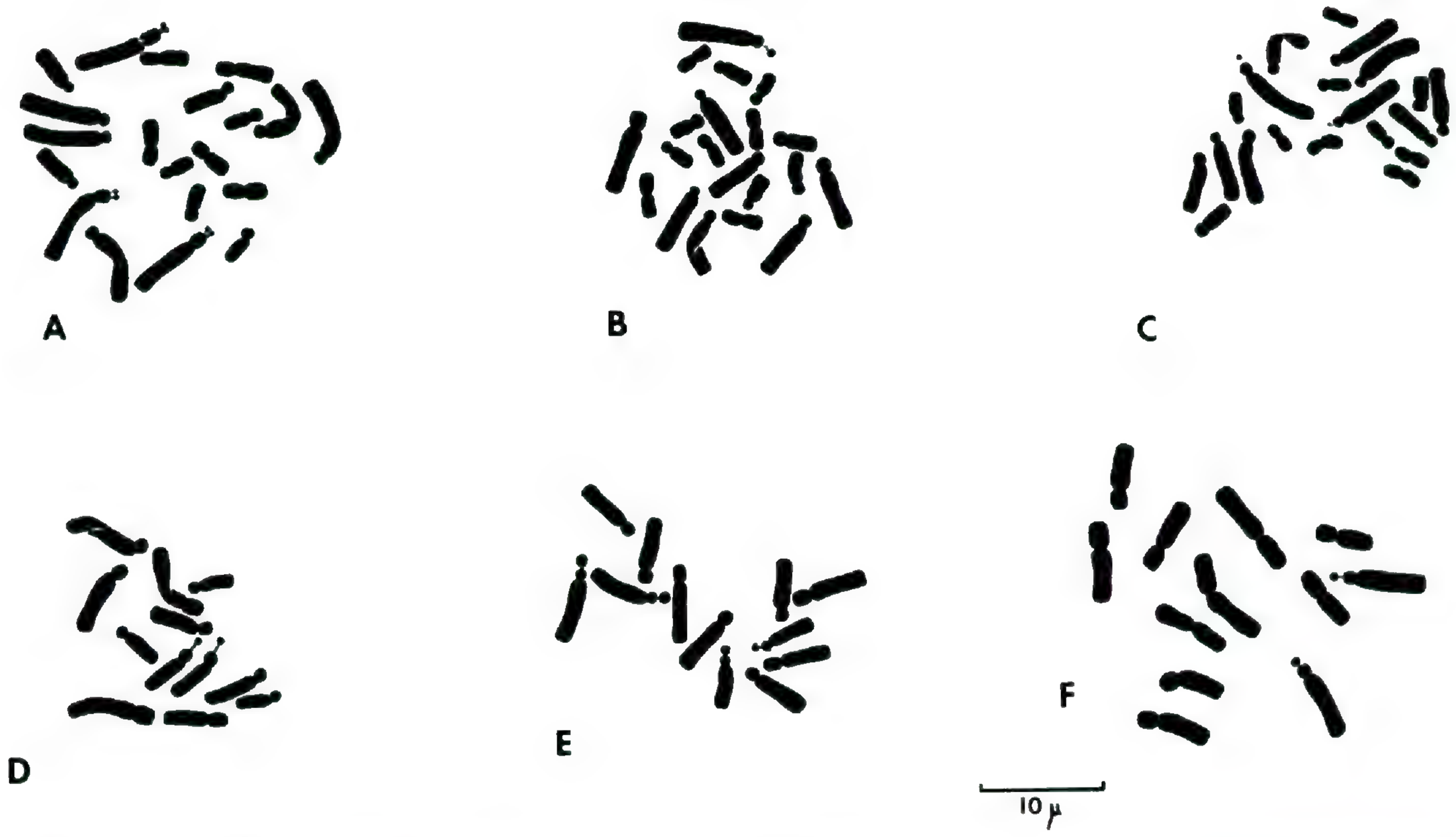


FIGURE 1. Mitotic metaphase figures.—A. *Moraea hexaglottis.*—B. *M. rigidifolia.*—C. *Barnardiella spiralis* for comparison (count but not figure reported in Goldblatt, 1976c).—D. *M. crispa.*—E. *M. pseudospicata.*—F. *M. worcesterensis.* (All to same scale.)

MORPHOLOGY

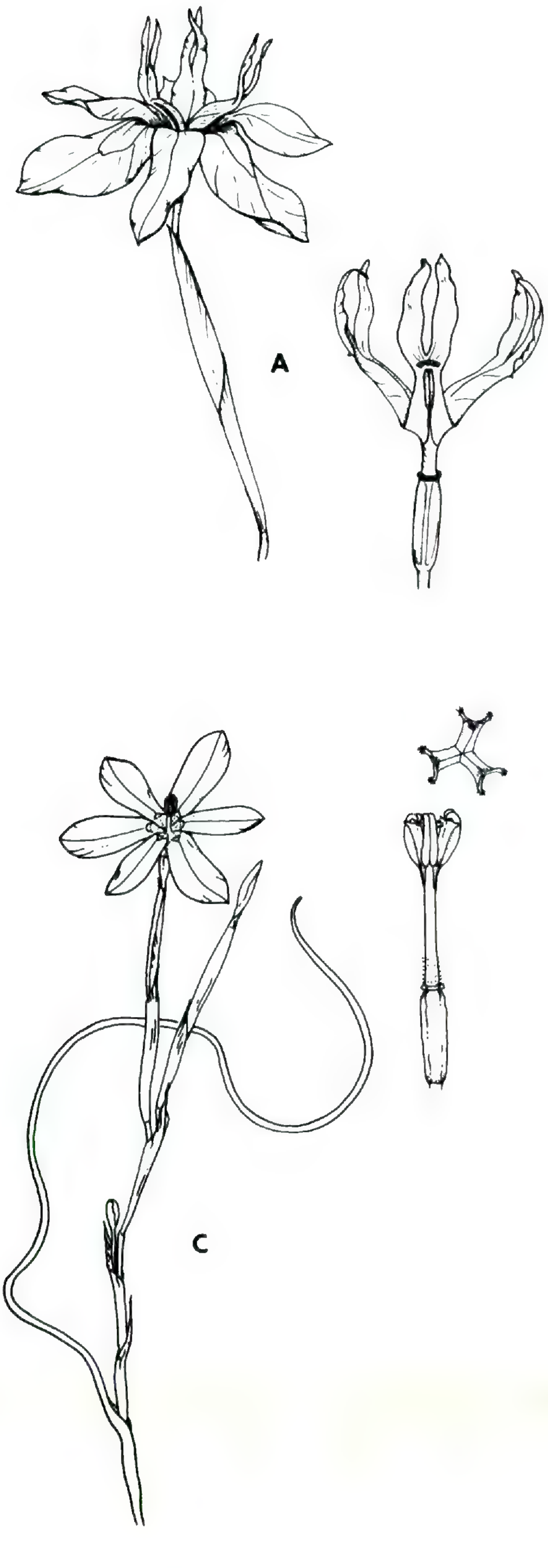
THE BASIC *MORAEA* FLOWER

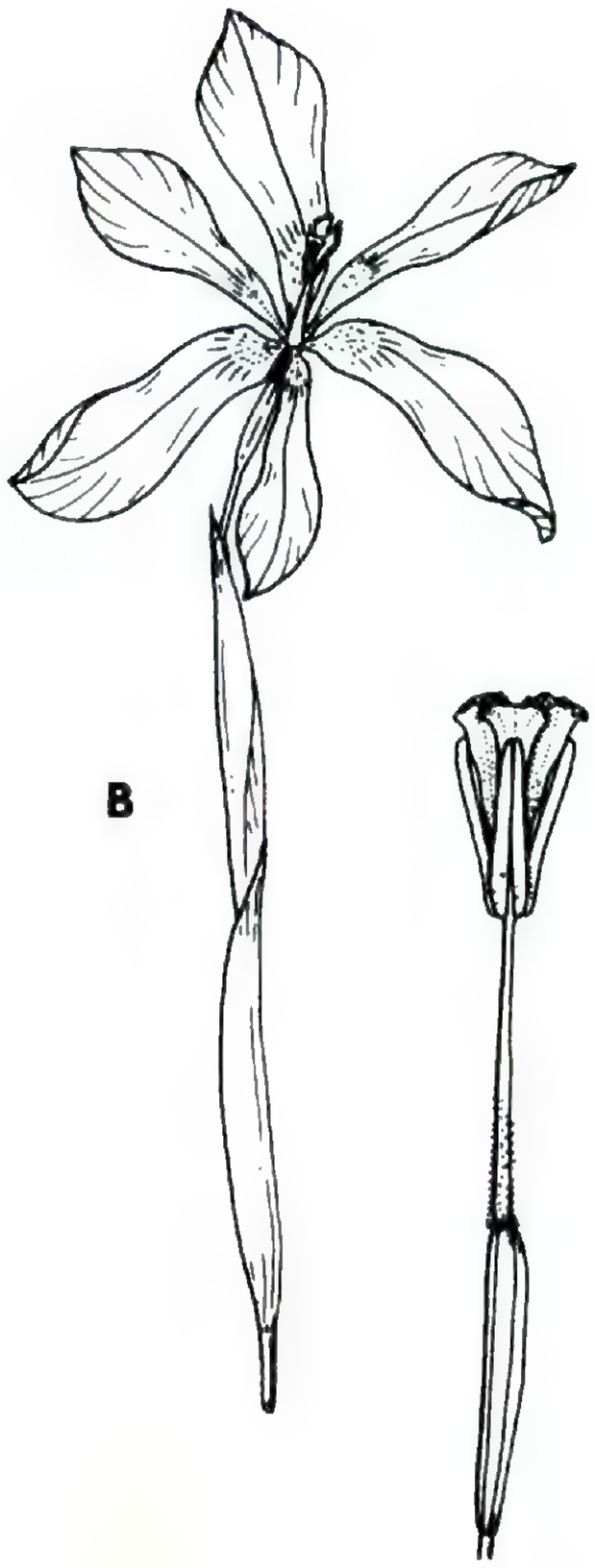
The typical and apparently basic *Moraea* flower has petal-like, flattened and broad style branches (Fig. 2A) that diverge from the style just above the apex of the filament column. Each style branch has a broad, transverse stigmatic lobe on the upper abaxial surface, and above the stigma it continues as a pair of flat erect appendages, the style crests. These elaborate style branches are like those found in the related *Iris* and *Dietes,* the latter believed to be ancestral to both *Moraea* and *Iris* (Goldblatt, 1981a). The *Moraea* flower is *Iris*-like also in having each stamen appressed to the opposed style branch and concealed by the claw of the outer tepal. The outer tepal is somewhat to much larger than the inner and always has a nectar guide at the base of the limb and a well-developed nectary at the base of the claw. The outer and inner tepals may be similarly oriented or the inner may be erect, or somewhat to very reduced, and then trilobed, aristate, ciliate, or completely lacking. In most species of *Moraea* the filaments are united in the lower half into a column around the style, but at least in subg. *Visciramosa* and in *M. ramosissima* (subg. *Moraea*) the filaments are contiguous but entirely free.

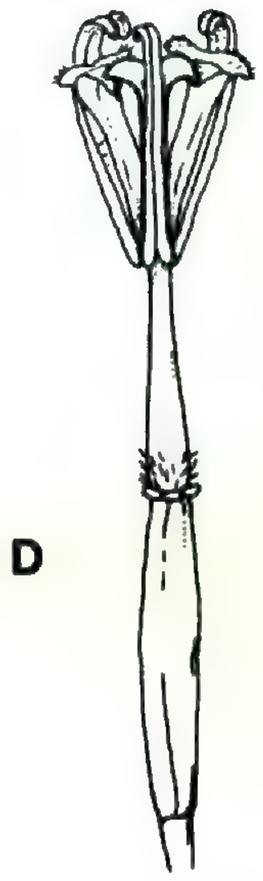
THE *HOMERIA* FLOWER

In *Homeria* (31 spp.) the flower is an apparently simple structure (Fig. 2B, D, E). It combines the derived features of united or nearly united filaments and broad tepal claws, which form a cup-like structure including or enclosing all or part of the stamens, as contrasted with apparently unspecialized subequal, similarly disposed inner and outer tepals, and style branches that either lack or have weakly developed paired crests. In addition both whorls of tepals have nectar guides at the base of the limbs and both have nectaries at the base of the claws. In *Homeria* the flower is known to be adapted for fly pollination (Goldblatt, 1981b). Several members of the genus are visited by species of Diptera and not by bees, which pollinate the flowers of most species of *Moraea.* However, some species of *Homeria,* in which the tepal claws are very short and the anthers are held well above the tepals, are secondarily adapted to bee pollination (Goldblatt, 1981b).

Until recently (Goldblatt, 1976a, 1980) all species of Homeriinae with the type of flower







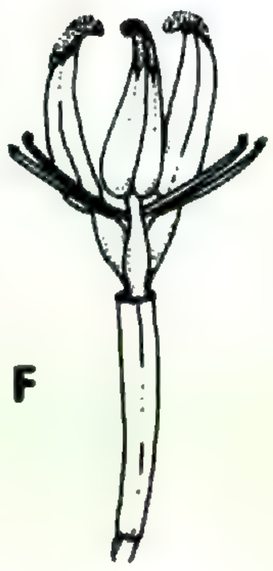


FIGURE 2. Floral features of species of *Moraea* and *Homeria*.—A. *Moraea bipartita*, as typical unspecialized flower typical of *Moraea*, the style branches and stamens drawn separately and enlarged.—B. *Homeria patens*, a typical *Homeria*.—C. *M. crispa*, with a flower modified in a manner similar to *Homeria*, the style branches and stamens much enlarged.—D. Style branches and stamens only of *Homeria elegans*.—E. *H. bifida*.—F. the related genus *Hexaglottis*, especially for comparison with *M. hexaglottis*. Whole flowers life size; separate style branches and stamens, ×2.

described above were assigned to *Homeria* despite a lack of uniformity in details of stem, leaf, and corm tunic morphology. Then as a result of a study of chromosome cytology and crossing relationships of the Homeriinae (Goldblatt, 1976a, 1980), it became clear that *Homeria* as defined by its characteristic flower alone was artificially constituted and polyphyletic. Information on cytology, interspecific hybridization, and vegetative structure resulted in the transfer of species with $n = 6$ and karyotypes matching those found in *Moraea* sect. *Polyanthes* to that section; the species with $n = 10$ were assigned to a new genus *Rheome* that was assumed to be derived from some extinct or at least not yet identified ancestor in *Moraea*.

THE NEW SPECIES

The Namib species and *Moraea pseudospicata* resemble the widespread Karoo *M. crispa* (Fig. 2C) in their small, pale to deep blue-purple flowers with short style branches, partly free filaments, and short tepal claws that form a cup including the base of the filament column. The flowers of all these species are extremely fugacious and open after 3 P.M. (even up to 5 P.M.) and fade soon after dark. Only *M. pseudospicata*, with $n = 6$, corresponds with *M. crispa* in chromosome number and karyotype, and it seems likely that the two are closely allied. It can be distinguished from *M. crispa* by its sessile lateral inflorescences, large corms with accumulated tunics, and small, globose, irregularly dehiscing capsules.

The three Namib species, all with $n = 10$, are regarded as unrelated to *M. crispa* because of the difference in karyotype and are presumed to be allied to species of sect. *Moraea* (or possibly the closely related sect. *Deserticola*), which also have $x = 10$ and a similar karyotype of four to five long acrocentric pairs and five to six much smaller pairs. *Moraea rigidifolia* has a thick, relatively short and rigid leaf, sessile lateral inflorescences, and fusiform, included ovaries (Fig. 6); *M. graniticola* is acaulescent and has a well-developed perianth tube and a rostrate, fusiform ovary (Fig. 3); and *M. hexaglottis* has short deeply divided style branches, the arms of which extend horizontally below the anthers. The morphological differences between the three Namib species suggest that they are not immediately related to one another. *Moraea rigidifolia* shares its terete leaf and sessile lateral inflorescences with the monotypic *Barnardiella* (Goldblatt, 1976c), and it is a possible link between this isolated genus and sect. *Moraea*. The immediate relationships of *M. graniticola* and *M. hexaglottis* are not apparent and their possible relationships and origins are discussed in the systematic treatment.

Moraea deserticola resembles the western Karoo *M. speciosa* in its flower and general appearance. Its cytology is not known but it seems certain that it is closely related to *M. speciosa* with which it probably shares a common origin from the widespread southern African *M. polystachya* or its immediate ancestors.

Moraea worcesterensis has $n = 6$ and a karyotype that corresponds well with species of sect. *Vieusseuxia*. It is perhaps most closely related to *M. algoensis* of this alliance, with which it shares a long-lasting, deep blue-purple flower, a slender few-branched stem, and heavily clawed, light brown corm tunics. Its affinity with sect. *Vieusseuxia* has been further established by successful crosses with *M. tripetala*, allied to *M. algoensis*. Control crosses with *M. bipartita* (sect. *Polyanthos*) did not succeed.

Thus, among these six new species of *Moraea*, there appear to be three separate assemblages with a broadly similar *Homeria* type flower. Additional groups with this type of flower are subg. *Visciramosa* (*M. elsiae* Goldbl.), subg. *Vieusseuxia* (including *M. thomsonii* Baker of sect. *Polyanthes*), and some isolated species of sect. *Vieusseuxia* (e.g., *M. lurida* Ker, *M. neopavonia* R. Foster, and *M. insolens* Goldbl.) in which the flower is less obviously *Homeria*-like.

ORIGIN AND ADAPTIVE VALUE OF THE FLOWER

There seems little doubt that the *Homeria* flower-type arose several times in the history of the *Moraea–Homeria* alliance. It is interesting and probably significant that there does not appear to be a progression of intermediate forms leading to the apparently complex and integrated set of features that comprise the flower. Instead, it seems to have arisen abruptly and it seems likely that one or a very few genic mutations have produced a phenotype so different that the result superficially appears to merit at least species or even generic segregation. The independent origin of similarly structured and colored flowers, even with similar flowering phenology in several species, mostly in the arid interior of western southern Africa suggests that there is some direct adaptive value to this flower. I can only speculate

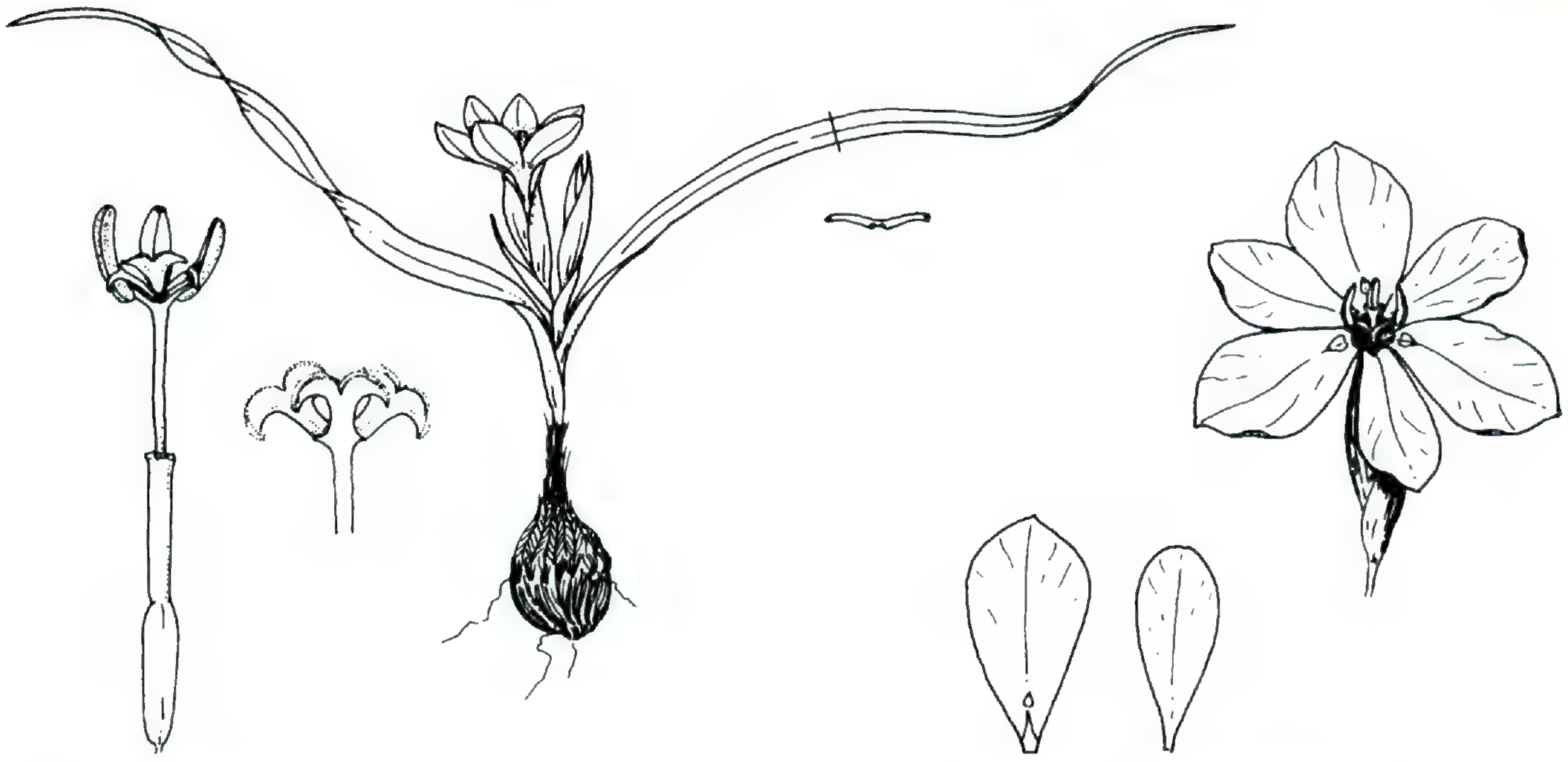


FIGURE 3. Morphology of *Moraea graniticola*. Whole plant, ×0.5; flower, separated tepals, and leaf transection, life size; gynoecium and androecium, ×2; separated style branches, much enlarged.

that the color is attractive to small bees, the most likely pollinators. Flowering late in the day may strengthen the chances for pollination at a time when other nectar and pollen sources have been exhausted. Fugaciousness probably protects the flower by limiting its exposure to desiccation and predation from herbivores for the least possible time, still allowing for cross pollination. Like nearly all members of Homeriinae, the new species are strongly self-incompatible (the condition in *M. deserticola* is not known).

SYSTEMATIC TREATMENT

SECTION *MORAEA*

1. Moraea graniticola Goldbl., sp. nov. TYPE: Namibia. Aus (26.16): southern Namib Desert, Aus townlands, in sand around granite domes, ca. 1,300 m (cult. Kirstenbosch Botanic Gardens in 1983) (CB), *Lavranos & Pehlemann 20007* (holotype, WIND; isotype, MO). FIGURE 3.

Plantae parvae plus minusve acaulescentes, foliis duobus secundo parvo vel vestigiale, caule ramis prope terram fasciculatis, floribus caeruleis, tubo ca. 5–6 mm longo, tepalis 16–20 mm longis, unguibus partem inferiorem columnae filamentorum includentibus, limbis horizontalibus extensis, filamentis 5–6 mm longis in columna connatis supra ad 1 mm liberis et divergentibus, antheris ad 3.5 mm longis divergentibus, ovario fusiforme rostrato 7–8 mm longo, ramis styli ad 2 mm longis bifurcatis quam antheris brevioribus.

Plants, low, acaulescent or nearly so, to 5 cm high. *Corm* 2.5–3.5 mm diam., with dark brown, coarsely fibrous tunics, live corm to 8 mm diam. *Leaves* usually 2, the second small and vestigial, grey-green, channeled, spreading, white in the midline, somewhat twisted, margins undulate, to 20 cm long and 6 mm wide. *Stem* subterranean or produced just above the ground, usually with 1–3 branches clustered near the base. *Inflorescence spathes* herbaceous, 2.5–3 cm long, the inner somewhat membranous and slightly shorter. *Flower* with a perianth tube, blue-violet with yellow nectar guides, tepal claws ascending and enclosing the lower part of the filament column, limbs spreading horizontally; *perianth tube* 5–6 mm long, white; *outer tepals* 18–20 mm long, obovate, 9–11 mm wide, claws to 3 mm long, the inner to 17 mm long and 9 mm wide. *Filaments* 5–6 mm long, united in a white cylindrical column, free and diverging in the upper 1 mm; *anthers* to 3.5 mm long, diverging, cream. Ovary 7–8 mm long, fusiform, included in the spathes, with a short sterile beak to 2 mm long; *style* dividing near the base of the anthers, branches diverging, 2 mm long, deeply bilobed, the lobes diverging, to 1 mm long, stigmatic towards apices. Capsule unknown. *Chromosome number* $2n = 20$ (*Lavranos & Pehlemann 20007*).

Flowering time. September to early October (in cultivation).

Distribution. Southern Namib Desert, in sand around granite domes, known only from around Aus. Figure 5.

Relationships. The flower of *Moraea graniticola* resembles closely those of *M. crispa, M. pseudospicata,* and *M. rigidifolia,* but as outlined in the introduction, the vegetative morphology and chromosome cytology indicate that the resemblance is due to convergence. It seems most likely that *M. graniticola* is most closely related to sect. *Moraea* in which all species except *M. rigidifolia* and *M. hexaglottis* have a typical *Moraea* flower with well-developed style branches and crests. However, it differs from all members of this section in having the perianth and filaments united below into a short tube. The tube is completely closed and apparently functions to raise the flower above the spathes for better display to pollinators. The acaulescent habit is unknown elsewhere in the section and is rare in *Moraea,* being restricted to the four species of sect. *Acaules.* This is an apparently monophyletic alliance distinguished by contractile pedicels that raise the tubeless flowers above the spathes and later draw them back for the completion of fruit development. It seems unlikely on morphological grounds that *M. graniticola* is related directly to *M. rigidifolia* despite the similarity of their subequal, short-clawed spreading tepals and short, narrow crestless style branches.

History. *Moraea graniticola* was discovered in 1982 by John Lavranos and Inge Pehlemann in a sterile state, in dry ground around granite boulders on the townlands at Aus, in southern Namibia. The town lies inland from Luderitz on the rail line to the interior, and towards the inner edge of the Namib Desert. Corms given to Kirstenbosch Botanic Gardens flowered in 1983 when the specimens that comprise the type collection were prepared. *Moraea graniticola* is apparently rare in the wild, even at the single site from which it is known. It is likely that the species occurs elsewhere in rocky parts of the southern Namib where there is normally some winter precipitation.

2. Moraea hexaglottis Goldbl., sp. nov. TYPE: Namibia. Witpütz (27.16): southern Namib, farm Aub, Huib Plateau, ca. 80 km N of Rosh Pinah, 1,200–1,400 m (BB), *Lavranos & Pehlemann 21704* (holotype, MO; isotype, WIND). FIGURE 4.

Plantae parvae, 8–10 cm altae, folio solitario gracili, caule ramoso, floribus caeruleis, tepalis ca. 10 mm longis, unguibus partem inferiorem columnae filamentorum includentibus, limbis horizontalibus extensis, filamentis 3 mm longis in columna connatis supra ad 1 mm liberis et divergentibus, antheris ad 2.5 mm longis divergentibus, ovario cylindrico anguste, ca. 3 mm longo, ramis styli bifurcatis a basi, ramulibus ad 2 mm longis, inter apices filamentorum extensibus.

Plants small, 8–10 cm high. *Corm* 10–15 mm diam., with coarse brown fibrous tunics. *Leaf* solitary, basal, slender, and apparently terete but linear and channeled, with tightly inrolled margins, sometimes somewhat twisted above, about twice as long as the plant. *Stem* somewhat flexuose, 1–2-branched, stem bracts subtending the branches 12–18 mm long, herbaceous, becoming dry above, axes flexed slightly below the spathes. *Inflorescence spathes* green, becoming dry and pale straw colored above, 16–19 mm long, the outer about half to nearly as long as the inner. *Flowers* blue-violet with pale yellow nectar guides on outer tepals; *outer tepals* 12–14 mm long, claw vestigial, limb spreading almost from the base, 6–7 mm wide, obovate; *inner* smaller than the outer, 10–12 mm long, lanceolate. *Filaments* ca. 4 mm long, united in the lower half in a smooth cylindrical column, diverging above; *anthers* 3–4 mm long, ascending, yellow. Ovary narrow, cylindric, ca. 3 mm long, at least partly exserted from the spathes; *style* dividing at the apex of the filament column, branches divided almost to the base into paired slender tapering arms extending upwards between the filaments, the arms 2.5–3 mm long, apically stigmatic, crests lacking. *Capsules* globose, 4–6 mm diam.; *seeds* angular. *Chromosome number* $2n = 20$ (*Lavranos & Pehlemann 21704*).

Flowering time. September to October, flowers opening in mid-afternoon, at about 4 P.M., fading in early evening.

Distribution. Known from only one site on the Huib Plateau at about 1,300 m, in southern Namibia in silt on black limestone. Figure 5.

Relationships. The small, blue-violet flowers with spreading, subequal tepals of *Moraea hexaglottis* are very like those of *M. rigidifolia* and the Karoo species *M. crispa.* However, the short style branches, each divided almost to the base into a pair of slender, ascending arms are unlike those of any other species of *Moraea* and resemble those of the related genus *Hexaglottis* (5 spp.). In *Hexaglottis* the filaments are united only towards the base and the style arms are more slender than in *M. hexaglottis,* and the flowers are always yellow. In addition, *Hexaglottis* has $x = 6$ (Goldblatt, 1971, and in prep.) in contrast to $n = 10$ in *M. hexaglottis.* It is clear that *M.*

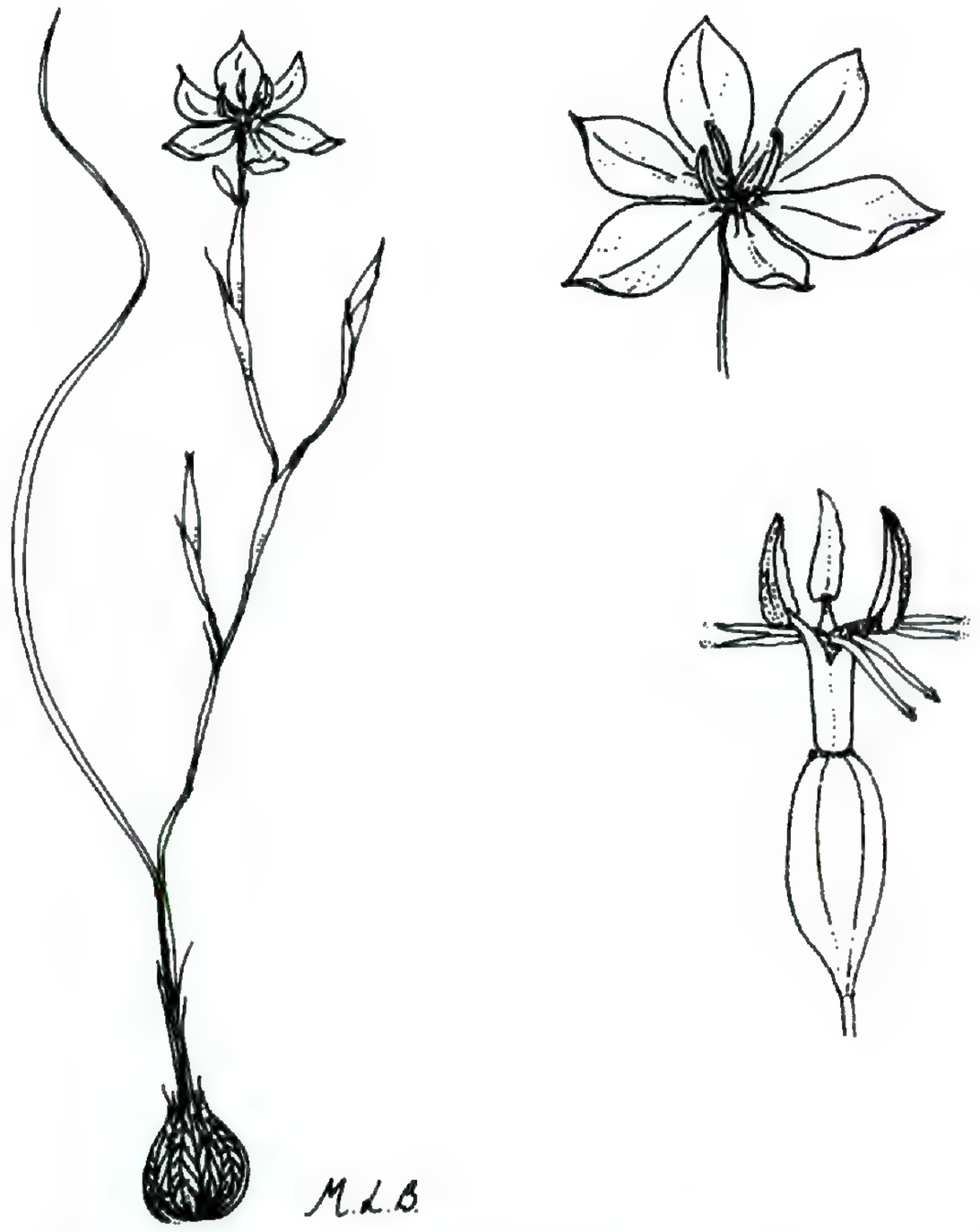


FIGURE 4. Morphology of *Moraea hexaglottis*. Whole plant, ×0.5; flower, life size; gynoecium and androecium, ×2.

hexaglottis and *Hexaglottis* acquired similar style branches independently, but the similarity is striking. *Moraea hexaglottis* is probably most closely related to *M. tortilis* of sect. *Moraea* based on overall similarity in vegetative morphology.

History. The species was discovered by John Lavranos and Inge Pehlemann in 1983 on the Huib Plateau in southern Namibia. It is known from a few sites on the farm Aub and is, according to Lavranos, widespread there. It probably occurs elsewhere on the western part of the Huib Plateau that receives limited precipitation in the winter. The habitat is described as silt on black limestone, quite different from the rocky granite where the other two southern Namibian species grow. The specific epithet refers to the six slender style arms or tongues that are characteristic for the species.

3. Moraea rigidifolia Goldbl., sp. nov. TYPE: Namibia. Witpütz (27.16): southern Namib Desert, rocky granite flats ca. 40 km N of Rosh Pinah, farm Süd Witpütz, ca. 1,100 m (DA), *Goldblatt 7016* (holotype, WIND; isotypes, MO, NBG, PRE, S, US, WAG). FIGURE 6.

Plantae 7–12 cm altae, folio solitario fistuloso falcato ad recurvo, caule inflorescentibus lateralibus sessilibus, raro infra ramoso, floribus caeruleo-malvinis, tepalis 13–18 mm longis, unguibus partem inferiorem columnae filamentorum includentibus, limbis horizontalibus extensis, filamentis 4–5.5 mm longis, in columna connatis supra ad 1.3–2 mm liberis et divergentibus, antheris 2.2–3 mm longis divergentibus, ovario lineari-fusiforme rostrato 5–7 mm longo, ramis styli 2–2.5 mm longis bifurcatis quam antheris brevioribus.

Plants slender, 7–12 cm high. *Corm* 2–3 cm diam., with dark brown, coarsely fibrous tunics accumulating to form a thick layer and extending upwards in a neck, live corm ca. 8 mm diam. *Leaf* solitary, basal, terete, to 3 mm diam., fistulose, pithy inside, falcate to recurved. *Stem* simple or branched from below, bearing several sessile inflorescences above, stem bracts dry, brown, to 2.5 cm long. *Inflorescences* sessile except the terminal, *spathes* herbaceous, becoming dry and brown above at anthesis, 1.7–2.2 cm long, the outer slightly shorter than the inner. *Flowers* blue-mauve with cream nectar guides on the outer tepals, the claws forming a shallow cup round the base of the filament column, limbs spreading horizontally; *tepals* lanceolate, 14–18 mm long, claw 3–4 mm, limb 6–7 mm wide, widest in the upper third, the inner 13–15 mm long, 5–6 mm wide. *Filaments* 4–5.5 mm long, united below, free in the upper 1.3–2 mm and diverging, forming a slender smooth cylindric column; *anthers* 2.2–3 mm long, diverging, white. Ovary linear-fusiform, included in the spathes, 5–7 mm long, with a sterile beak 1–2 mm long; *style* dividing at the apex of the filament column, branches diverging, 2–2.5 mm long, bilobed above and stigmatic apically, reaching to mid anther level, crests lacking. Capsules not known. *Chromosome number 2n* = 20 (*Goldblatt 7016*).

Flowering time. Late September to October, flowers opening in late afternoon, at about 4:30 P.M. and fading in early evening at about 7 P.M.

Distribution. Rocky granite flats, in the southern Namib Desert north of Rosh Pinah. Figure 5.

Relationships. The small, pale blue-mauve flowers of *Moraea rigidifolia* have subequal tepals with short claws that enclose the lower part of the filaments and divergent anthers appressed to short narrow style branches. They closely resemble those of the Karoo species *M. crispa*. My initial presumption was that the two were closely related. However, *M. rigidifolia* has a base num-

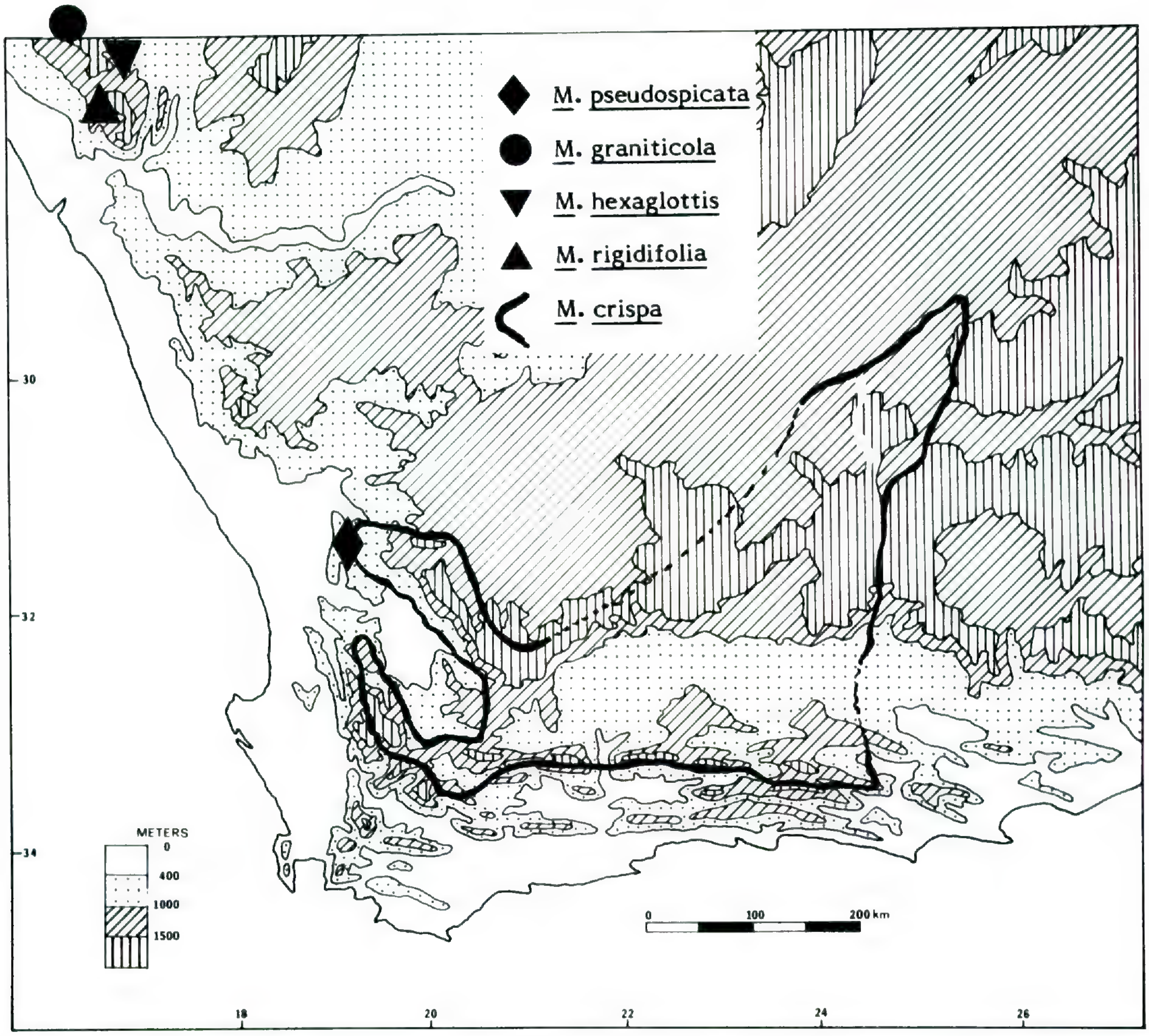


FIGURE 5. Geographical distribution of *Moraea pseudospicata, M. graniticola, M. hexaglottis, M. rigidifolia,* with the range of *Moraea crispa* heavily outlined for comparison.

ber of $x = 10$ and karyotype quite different from that of *M. crispa* and of sect. *Polyanthes* generally. The basic chromosome number for *Moraea* is $x = 10$ and both number and the details of the karyotype of *M. rigidifolia* conform with species of subg. *Moraea* as well as with the monotypic Namaqualand *Barnardiella*. The cytological evidence is regarded here as a more reliable indicator of relationship, and *M. rigidifolia* is presumed to be allied to species of sect. *Moraea* or sect. *Deserticola*. In its general habit *M. rigidifolia* resembles quite closely *Barnardiella spiralis*, which has similar, though more often smaller corms, a single terete but slender leaf, and sessile lateral inflorescences with relatively short and subequal spathes. *Barnardiella* differs in having a long slender tube composed of sterile ovary tissue (Goldblatt, 1976c) and a subsessile ovary located in the base of the spathes. Details of the style and anthers of *Barnardiella* differ only slightly from those of *M. rigidifolia* and it seems likely that *M. rigidifolia* is close to the line that gave rise to *Barnardiella*. The slender ovary of *M. rigidifolia*, which is sterile in the upper 1–1.5 mm, is perhaps a link with the unusual ovary found in *Barnardiella*.

Moraea rigidifolia is easily recognized by its very unusual thick and relatively short terete leaf. The swollen leaf, which consists of green tissue surrounding a firm white pith-like parenchyma, is so striking that *M. rigidifolia* can immediately be identified from this feature alone.

Distribution. *Moraea rigidifolia* is known only from a single locality in southern Namibia, on

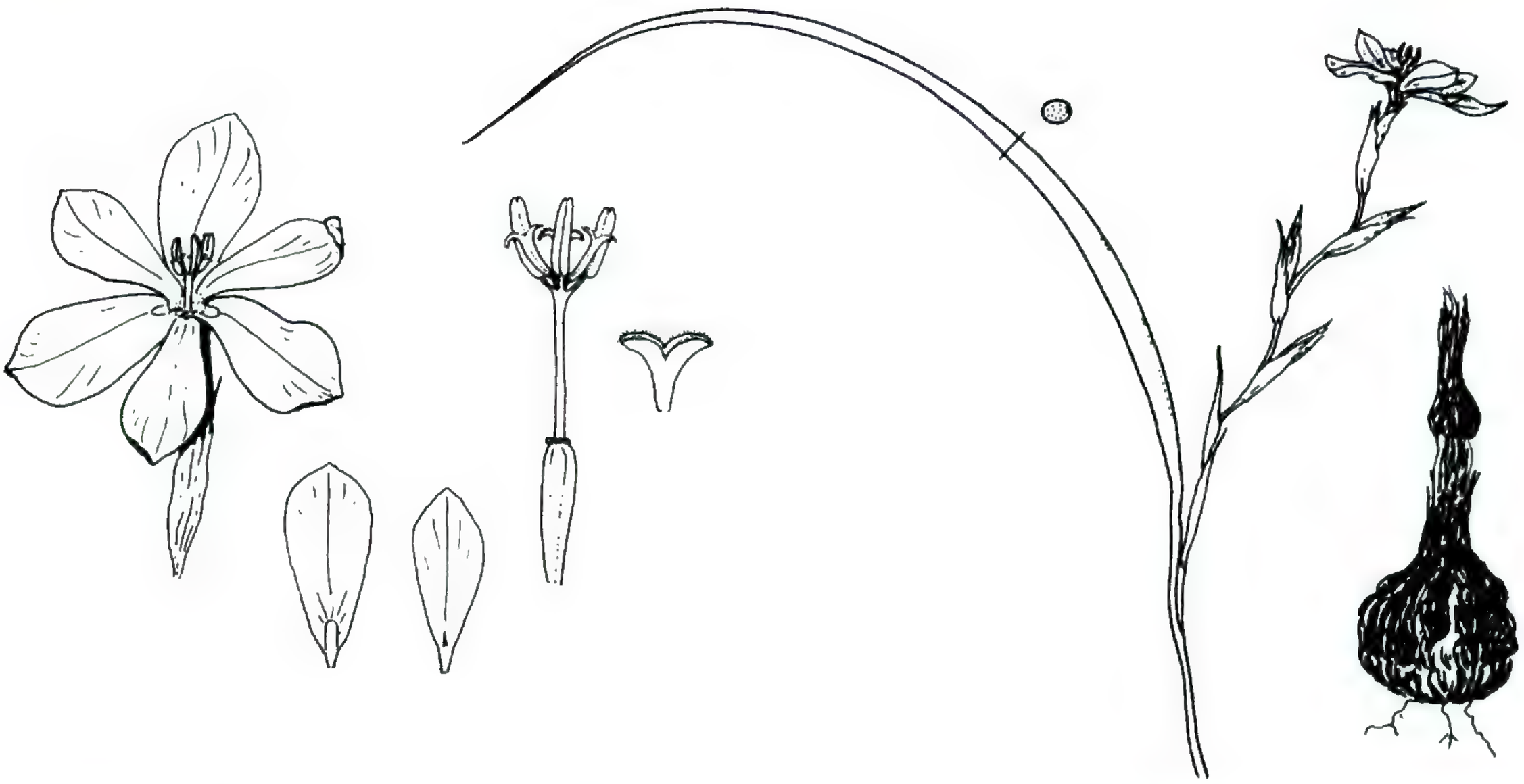


FIGURE 6. Morphology of *Moraea rigidifolia*. Whole plant, corm, and leaf transection, ×0.5; flower and separated tepals, life size; gynoecium and androecium, ×2; separated style branch, much enlarged.

the farm Süd Witpütz, some 35 km north of the mining settlement of Rosh Pinah near the Orange River. It was discovered by John Lavranos and Inge Pehlemann in 1982. In the very good spring season of 1983 I revisited the locality and collected ample flowering specimens. The habitat of *M. rigidifolia* is rocky and consists of thin soil and low outcrops of weathered granite. It is locally fairly common in open places, the corms often wedged in cracks in rock, but only shallowly buried. *Moraea rigidifolia* probably occurs elsewhere in the rocky southern Namib Desert, which is poorly known botanically. Owing to its inconspicuous and fugacious flowers that open only in the late afternoon and early evening, it is easily overlooked.

Additional material examined. NAMIBIA. Southern Namib Desert. 29.16 (Witpütz) rocky granite flats ca. 40 km N of Rosh Pinah, farm Süd Witpütz, ca. 1,100 m (DA), *Lavranos & Pehlemann 19104* (MO).

SECTION *POLYANTHES*

4. Moraea pseudospicata Goldbl., sp. nov. TYPE: South Africa, Calvinia (31.19): Cape Province, Glenlyon, E of Nieuwoudtville, dry Dwyka tillite flats (AC), *Snijman 783* (holotype, NBG; isotypes, K, MO, PRE, S, STE, WAG). FIGURE 7.

Plantae 15–40 cm altae, folio solitario gracili canaliculato in latere adaxiali, caule interdum infra ramoso, inflorescentibus lateralibus sessilibus, floribus caeruleo-malvinis, tepalis 11–16 mm longis, unguibus partem inferiorem columnae filamentorum includentibus, limbis horizontalibus extensis, filamentis 4–6.5 mm longis, in columna connatis vel supra liberis et contiguis, antheris 2–4.5 mm longis contiguis, ovario globoso ca. 2 mm diam., ramis styli 1–1.5 mm longis antheris occultis.

Plants slender, 15–40 cm high. *Corm* 3–5 cm diam., with tough, blackish fibrous tunics usually accumulating to form a thick layer and extending upwards in a neck, live corm ca. 1 cm diam. *Leaf* solitary, basal, slender, apparently terete but narrowly grooved on adaxial surface and margins tightly inrolled, straight or weakly twisted. *Stem* simple or 1–2-branched from below, bearing several sessile inflorescences at the upper nodes, stem bracts dry, brown, to 2.5 cm long, distinctly darker on the veins. *Inflorescences* sessile except the terminal, *spathes* subequal, partly concealed by the subtending bracts, dry and straw-colored at anthesis, also darker on the veins, 2–2.5 cm long. *Flowers* blue-mauve with deep yellow nectar guides on inner and outer tepals, the claws forming a shallow cup round the base of the filament column, limbs spreading horizontally; *tepals* lanceolate, 11–17 mm long, claw ca. 2 mm, limb 3.5–4 mm wide, widest in the upper third, the inner tepals ca. 1 mm shorter than the outer. *Filaments* 4–6.5 mm long, united entirely or free in the upper two-thirds but contiguous, forming a slender, smooth cylindric column; *anthers* 2–4.5 mm long, erect and contiguous, yellow. Ovary

FIGURE 7. Morphology of *Moraea pseudospicata*. Whole plant and corm, ×0.5; flower and separated inflorescence with fruit, life size.

globose, ca. 2 mm long; *style* dividing at about mid anther level, branches narrow, ascending, 1–1.5 mm long, stigmatic apically, initially concealed by the anthers, reaching to the upper third or slightly exceeding the apex of the anthers; crests lacking. *Capsules* globose, 2–4 mm diam., membranous and semitransparent, not loculicidal but fragmenting irregularly; seeds several, dark brown, ca. 1 mm long. *Chromosome number* $2n = 12$ (*Goldblatt 6543*).

Flowering time. December to March, flowers opening after 3:30 P.M. and fading in the early evening.

Distribution. Rocky clay flats, in karroid scrub, in the Nieuwoudtville district from the hills north of the town extending south to Lokenberg and possibly to the dry interior valleys of the Cedarberg. Figure 5.

Relationships and variation. Moraea pseudospicata resembles the widespread Karoo species *M. crispa* in both flower structure and general aspect. The pale blue-mauve flowers are almost identical in their subequal tepals with short erect claws that form a short, narrow tube, which includes the lower part of the filament column. The filaments and anthers are slightly shorter in *M. pseudospicata,* and the anthers are nearly erect and so conceal the narrow and short style branches. In *M. crispa* the anther and style branches diverge strongly, and although the style branches are shorter than the anthers, they can easily be seen. The two species also have the same chromosome number, $n = 6$, and karyotypes with acrocentric to submetacentric chromosomes that characterize sect. *Polyanthes,* and it seems certain that the two are closely allied. *Moraea pseudospicata* differs mainly in its sessile lateral inflorescences and in the dry chaffy stem bracts and spathes. Its capsules also differ from those of *M. crispa* in being slightly smaller, in having almost membranous walls, and in apparently dehiscing irregularly rather than along the locule sutures as in nearly all other species of *Moraea. Moraea pseudospicata* is also distinctive in its flowering time, mid to late summer, in an area of complete summer drought, and at the time of flowering the leaf is usually dry and often broken. In the summer dry western Karoo and adjacent Cedarberg where both *M. pseudospicata* and *M. crispa* occur, *M. crispa* blooms from October to November and rarely into December.

The relatively few collections of *Moraea pseudospicata* indicate little variability except for the filaments, which may be almost entirely united or free but contiguous in the upper half. This feature does not appear to be correlated with geographical distribution.

An unusual collection, *Galpin 11170* (K, PRE), from Nieuwoudtville, has a strong resemblance to *Moraea pseudospicata.* It has small but apparently deep blue-purple flowers and the characteristic sessile lateral inflorescences of *M. pseudospicata,* but the capsules, of which there are several in nearly mature state, are elongate and fusiform, about 10 mm long, and have a well-developed beak about 1 mm long. This is quite different from the globose capsule of *M. pseu-*

dospicata. Examination of the poorly preserved and few flowers reveals that the filaments are 3.5 mm long, and at least free above (indistinct below), the anthers are contiguous and very short, about 1.2 mm long, and the ovary is about 4.5 mm long. Other details are not visible. It seems likely that the collection represents a species closely allied to *M. pseudospicata,* distinguished at least by a different capsule (that contains apparently larger seeds), smaller anthers, and darker colored flowers. The flowering time noted on the single collection is November, another difference with *M. pseudospicata,* which has not been recorded in flower earlier than December, and usually flowers later.

History. The first known collections of *Moraea pseudospicata* were made by Carl Zeyher, who in 1829 journeyed to Namaqualand (Gunn & Codd, 1981) and the mouth of the Orange River 'Reise nach Kamiesberg, Boschmanland, bis zur mundung des Garip.' Several duplicates, distributed as *Ecklon & Zeyher Irid. 32* are in herbaria that have good sets of Ecklon and Zeyher duplicates. Only the sheet at Stockholm has complete locality data 'Onderboksveld, Bluht December, 4 hohe.' From this it seems almost certain that their gathering was made near present-day Nieuwoudtville, this general area still being sometimes called the Lower Bokkeveld. Other early records of this species include plants from the 'Cedarberg,' collected by Thode and from Lokenberg, south of Nieuwoudtville, collected by Acocks. All these collections lay unidentified or placed with either *Hexaglottis* or *M. crispa.* In 1980 Dierdre Snijman of the Compton Herbarium at Kirstenbosch showed me a collection of a species she had made near Nieuwoudtville that included well-pressed flowers. The specimens struck me as unusual both in morphology and in their flowering time. In 1982 I relocated the species at two sites to the north of Nieuwoudtville and made extensive collections. Once this species had been identified as a new and distinctive *Moraea,* I was able to assign to it the earlier records cited above. Specimens were found at a third site closer to Nieuwoudtville in 1984, and this collection has been selected as the type material.

Additional specimens examined. SOUTH AFRICA. CAPE: 31.19 (Calvinia) near Nieuwoudtville, Charlies Hoek, between Loeriesfontein Road and Klipkoppies (AC), *Snijman 98* (NBG), *Goldblatt 6542* (MO); rocky clay flats on the road to Rondekop, E of Nieuwoudtville, *Goldblatt 6543* (MO, NBG, PRE, S); Glenlyon, E of Nieuwoudtville, dry Dwyka tillite flats (AC), *Snijman 783* (K, MO, NBG, PRE, S, STE, WAG); Lokenburg (CA), *Acocks 17555* (PRE).

WITHOUT PRECISE LOCALITY: "Reise nach Kamiesberg, Boschmanland, bis zur Mundung des Garip," *Zeyher* as *Ecklon & Zeyher Irid. 32* (73.12) (LD, MO, P, S 'Bluht December 4 hoh Onderboksfeld'); Cedarberg, *Thode A2076* (PRE).

5. Moraea deserticola Goldbl., sp. nov. TYPE: South Africa. Vanrhynsdorp (31.18): Cape Province, Knersvlakte, farm Quaggas Kop, Zout River (BC), *Hall 5089* (holotype, NBG; isotype, MO).

Plantae 35–45 cm altae, cormo ca. 1 cm diam., foliis 2–3 linearibus canaliculatis, floribus albis pallide caeruleis in reverso, unguibus cupulatis columnam filamentorum includentibus, tepalis 30–36 mm longis, filamentis 8–10 mm longis connatis in columna cylindrica, antheris 5–6.5 mm longis erectis contiguis, ovario plus minusve obovato, 6–7 mm longo, rubro venoso, ramis styli brevibus horizontaliter extensis supra antheras.

Plants 35–45 cm high. *Corm* ca. 1 cm diam., with tunics of dark brown to blackish fibers. *Leaves* 2–3, linear and channeled, 2–3 mm wide, about as long as the stems, margins becoming tightly inrolled when dry, the lower basal, upper cauline. *Stem* simple or 1–3-branched from the upper nodes, the branches subtended by sheathing bract leaves 2.5–4 cm long. *Spathes* 3.3–4 cm long, herbaceous, the outer about two-thirds as long as the inner. *Flowers* pale blue or white with pale blue on the reverse of the tepals and fading pale blue, with yellow nectar guides at the base of the limb of the inner and outer tepals, tepal claws ascending and forming a wide cup including the filament column, limbs extended horizontally; *tepals* 30–36 mm long, claw ca. 12 mm long, limb 18–20 mm long and 10–11 mm wide, the inner slightly smaller than the outer. *Filaments* 8–10 mm long, united into a smooth slender cylindrical column; *anthers* 5–6.5 mm long, erect, contiguous, appressed to and initially concealing the style. Ovary 6–7 mm long, narrowly obconic, exserted from the spathes, with conspicuous reddish veins; *style* dividing into 3 short horizontal lobed branches just above the apex of the anthers; branches ca. 1 mm long, crests lacking. *Capsule* more or less obovoid, 9–10 mm long, red-veined, seeds many, angled. *Chromosome number* unknown.

Flowering time. June to August.

Distribution. Stony slopes and flats in the Knersvlakte between Vanrhynsdorp and Nuwerus. Figure 8.

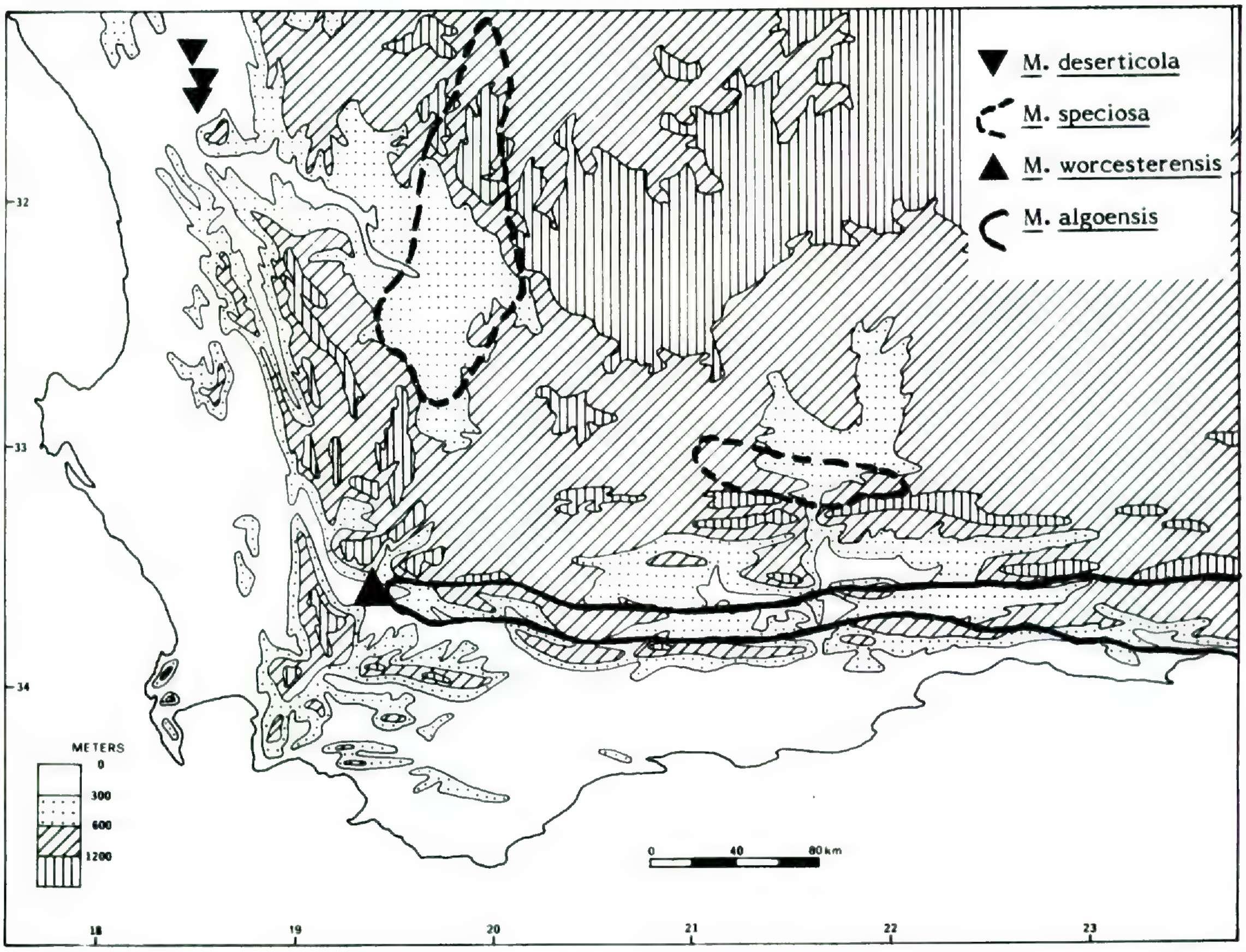


FIGURE 8. Geographical distribution of *Moraea deserticola*, with the range of the closely allied *M. speciosa* indicated by the broken line, and *M. worcesterensis*, with the range of the putatively related *M. algoensis* indicated by the heavy, unbroken line.

Relationships. The large and deeply cupped flower of *Moraea deserticola* with its nearly equal tepals and long conspicuous anthers is strongly reminiscent of *M. speciosa*, a species of the drier parts of the western Karoo. It seems certain that the two species are closely allied although they differ greatly in vegetative morphology. The long style surrounded by the contiguous anthers, and short, broadly-lobed style branches held above the anthers when the stigmas are receptive are exactly the same in both species. Except for a slightly smaller size, the flowers and all floral parts of *Moraea deserticola* are apparently identical to those of *M. speciosa*. The leaves of *M. deserticola* are narrow and few, and only the lowermost is basal while the other two or three are spaced well apart along the stem. Moreover, the leaves are straight and narrowly channeled and the stem bears only a few branches towards the apex. In contrast, *M. speciosa* has a thick fleshy well-branched stem and several relatively short and broad basal leaves that are often undulate or twisted. *Moraea deserticola* can also be distinguished by its strongly dark purple-veined ovary, a feature not evident in *M. speciosa*.

History and distribution. The species was first discovered in 1967 by P. A. B. van Breda, in the Knersvlakte, the arid low rolling country in southern Namaqualand that is so extraordinarily rich in low-growing succulents. Due to the limited material available and inadequate preservation, the collection could not at first be identified although it did not seem to be any known species. It was recollected in 1981 by Harry Hall and two years later by Jan Vlok but has not been seen since. The collection made by Hall is barely sufficient for a type but it seems preferable to describe the plant now rather than wait indefinitely hoping to find more specimens. Perhaps also now that the species is named others will be encouraged to search further for it.

The species is probably rare in the wild, but

as it has been found at three sites in the Knersvlakte, it probably occurs widely in the area. Most likely the plants are scattered and inconspicuous, and added to this, they probably flower only when good rains have fallen in this arid area.

Additional specimens examined. SOUTH AFRICA. CAPE: 31.18 (Vanrhynsdorp) 9 km NW of Vanrhynsdorp near the gypsum mines, sandy soil, *Vlok 655* (MO); Varsrivier, ca. 11 mi. N of Vanrhynsdorp, *van Breda 4018* (PRE).

SECTION *VIEUSSEUXIA*

6. Moraea worcesterensis Goldbl., sp. nov. TYPE: South Africa. Worcester (33.19): Cape Province, stony sandstone flats at Worcester West (CB), *Goldblatt & Snijman 6977A* (holotype, NBG; isotypes, K, MO, PRE, S, STE, US). FIGURE 9.

Plantae 12–25 cm altae, tunicis fibrosis unguiculatis, folio solitario canaliculato, floribus atropurpureis tepalis inaequalibus expansis, exterioribus 15–17 mm longis, interioribus 13–15 mm longis, unguibus ca. 3 mm longis, filamentis liberis supra, antheris 4 mm longis, ramis styli angustis apicibus bilobis.

Plants 12–25 cm high. *Corm* globose, 15–20 mm diam., tunics brown, fibrous, often heavily clawed, sometimes accumulating to form a thick covering. *Leaf* solitary, basal, linear, canaliculate, somewhat to about twice as long as the stem. *Stem* simple or with a single branch, erect or flexed at the upper nodes. *Spathes* herbaceous, dry and dark brown above, 28–35 mm long, the outer about half as long as the inner. *Flowers* dark violet-purple with yellow nectar guides on all tepals; *outer tepals* 15–17 mm long, claw ascending, ca. 3 mm long, limb laxly extended horizontally, 12–14 mm long and ca. 9 mm wide; *inner tepals* similarly oriented, smaller, 13–15 mm long and 4–5 mm wide. *Filaments* 5–6 mm long, united below, free in the upper 2 mm; *anthers* 4 mm long, exceeding the style branches, yellow. Ovary ca. 5 mm long, nearly cylindric but narrowing below, *style branches* narrow, less than 1 mm wide, diverging and appressed to the opposed anther, becoming bilobed apically and stigmatic at the ends of the lobes, *crests* lacking. *Capsules* narrowly obovoid, to 10 mm long. *Chromosome number* $2n = 12$ (*Goldblatt 6977A*).

Flowering time. September.

Distribution. Known only from stony flats west of Worcester, in mixed fynbos and renosterveld. Figure 8.

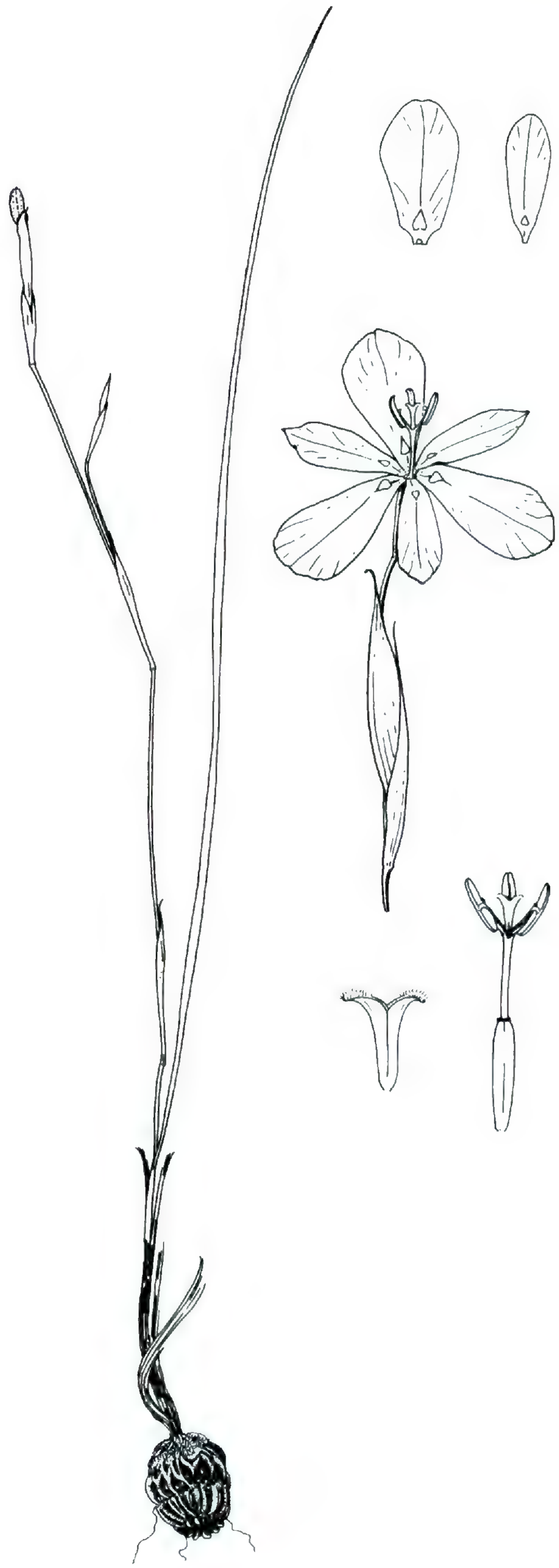


FIGURE 9. Morphology of *Moraea worcesterensis*. Whole plant, ×0.5; flower and separated tepals, life size; gynoecium and androecium, ×2; separated style branch, much enlarged.

Relationships. *Moraea worcesterensis* is probably closely related to the widespread southern Cape species *M. algoensis,* despite its very different flowers. It has more or less spreading tepals, both whorls of which have nectar guides, a slender filament column, and very reduced, narrow style branches, shorter than the subtending anthers and lacking crests. *Moraea algoensis* has a typical *Moraea* flower with large inner tepals, the claws of which touch the broad petaloid style branches to conceal the anther and stigma lobe. In *Moraea algoensis* the inner tepals are relatively broad for sect. *Vieusseuxia,* most species of which have narrow, linear, trifid to ciliate inner tepals. The general flower color of *M. worcesterensis* and *M. algoensis* is the same, and the corms conform to the type found in many species of the section. The single and basal leaf and reduced number of branches are also consistent with placement in this section.

The general similarity of *Moraea worcesterensis* to *M. polyanthos* in sect. *Polyanthes* is probably due to convergence for the *Homeria* type of flower. Thus although the flowers of the two species are similar, the vegetative structure is very different. *Moraea polyanthos* has (two to) three to five leaves, several branches, and blackish corm tunics of a tough wiry texture, all characteristics that seem to be significant in determining the relationships of species of *Moraea.*

History. *Moraea worcesterensis* was apparently first discovered in the spring of 1983, by me, Dierdre Snijman, and Jane Turnbull, both of the National Botanic Gardens, in Worcester West, a rapidly developing suburb of Worcester. It is now extinct at the type locality but probably occurs elsewhere along the foot of the Langeberg Mountains.

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THE CALYX IN *LYCIANTHES* AND SOME OTHER GENERA[1]

W. G. D'ARCY[2]

ABSTRACT

Vasculature and structure of calyces in *Lycianthes* and some related genera are analyzed to derive more generalized hypotheses on evolutionary trends in similar calyces. The generalized solanaceous calyx is seen as a whorl of five lobes enervated by five primary traces that branch in the lobes to form a pair of lateral veins and minor leaf-like venation. The adjacent laterals fuse basally to form an interconnector vein but are separate distally. There has been a tendency in these genera for the calyx lobes to fuse to higher levels, sometimes right to the top (perfect prefloration). There has been a tendency to fusion of lateral veins to higher levels, which gives rise to ten main traces or ribs in the fused area. The flower must egress from the bud and may do so in several ways. Where calyx prefloration is complete or nearly so, egress must involve stretching or tearing. Thus in *Lycianthes, Witheringia,* and *Capsicum,* the calyx becomes thin, with reduced, distorted venation under stretching stresses of floral egress in a region termed the sleeve. A tooth, here meaning any pointed structure accessory to a flower or inflorescence, is nearly ubiquitous in vascular plants, perhaps for protection. When the calyx teeth are completely fused, they no longer function as teeth. In some Solanaceae, this deficiency is remedied by enation of 'secondary' teeth below the sleeve. In *Lycianthes* they may be enervated by primary traces and fused laterals leading to the ten teeth in two series. These sequences of calyx evolution can be seen in some other families such as the Ericaceae.

In a group of genera in which the number of parts in a floral whorl is generally five, the frequent presence of ten teeth on the calyx of many *Lycianthes* species seems anomalous. These teeth are often in two alternating series and range in different species from small umbos to elongate, filiform processes many times the size of the calyx body. Closer examination discloses that these teeth are not apical on the calyx but appear from the side of the calyx below a ring or "sleeve" of tissue that terminates the calyx wall (Figs. 2–4, 7). Dunal (1852) grouped species like this into subsection *Lycianthes* of the genus *Solanum,* which was elevated to generic rank by Hassler (1917). The name *Lycianthes* was conserved over earlier names (McVaugh, 1973). Bitter (1919) and subsequent workers have expanded the genus to well over a hundred species. Placement of *Lycianthes* at the generic level was at first justified because of the reduced inflorescences and the presence of large stone cells in the fruit (Hassler, 1917; Bitter, 1914, 1919; Danert, 1969), yet the segregation of the group from *Solanum* has not met with the acceptance of all botanists. With a desire to understand the nature of the seemingly anomalous calyx structure and to reassess the validity of this genus, a study of calyx vasculature was undertaken. A considerable range of material in related genera of Solanaceae, especially in subfamily Solanoidae, was studied, and material from other families was also examined. Some patterns in the evolution of calyces in the Solanaceae are apparent in other unrelated families.

METHODS

Traditional methods using sodium hydroxide and chloral hydrate were used to clear fresh, pickled, and dried flower buds and calyces of selected Solanaceae, and this treatment was sometimes followed by staining with safranin or basic fuchsin. These methods gave good three-dimensional views under a binocular dissecting microscope when material was held in vials in liquid but generally yielded poor photographic subjects. For photographs it was sometimes necessary to flatten the material on a glass slide and add a cover slip. Series of stained microscope sections of *Capsicum annuum* L., *Solanum seaforthianum* Andr., and *Oryctes nevadensis* S. Wats. were used for comparison. In addition, a great many flowers from many families were examined by naked eye and hand lens in the herbarium and in a living state.

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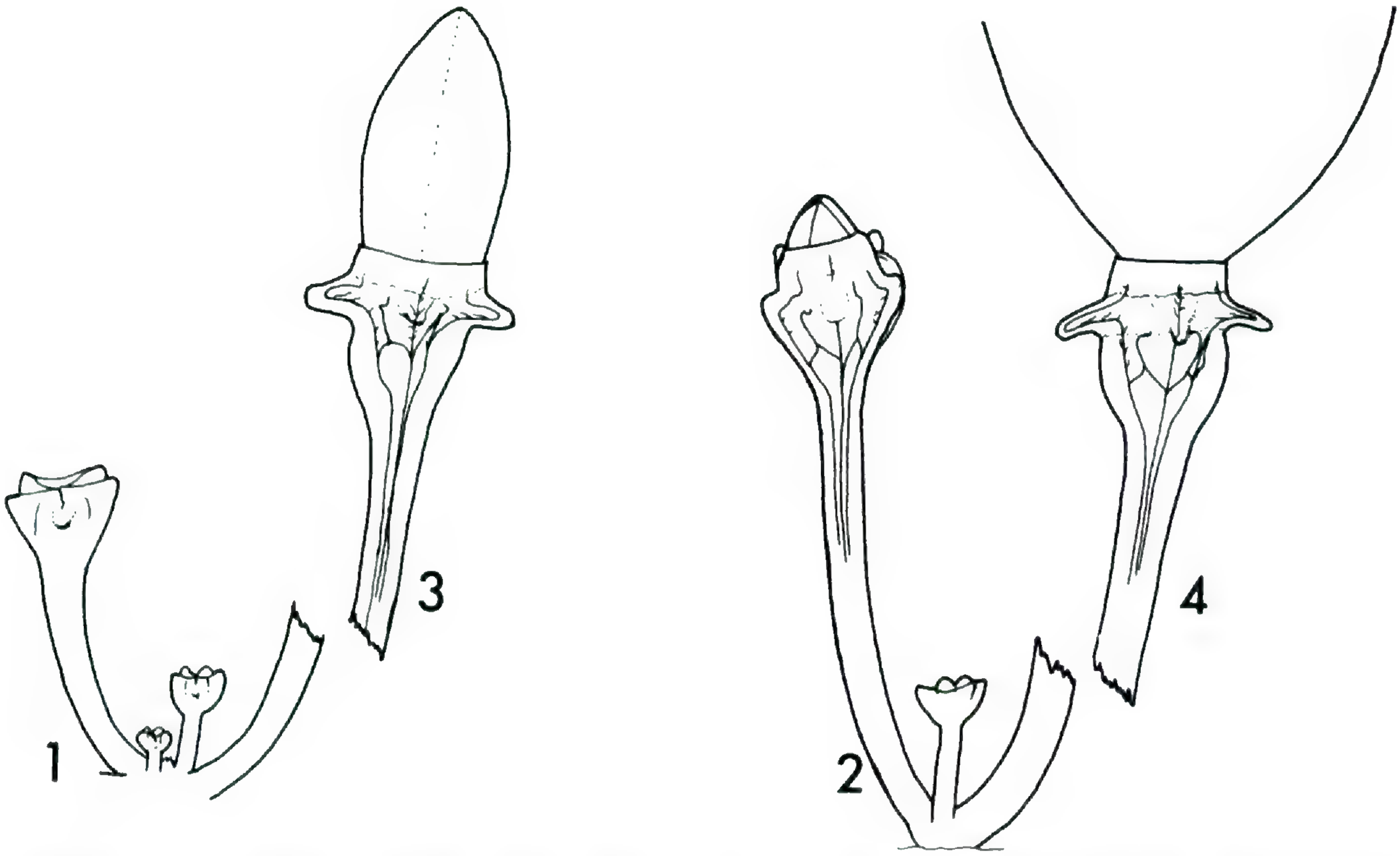
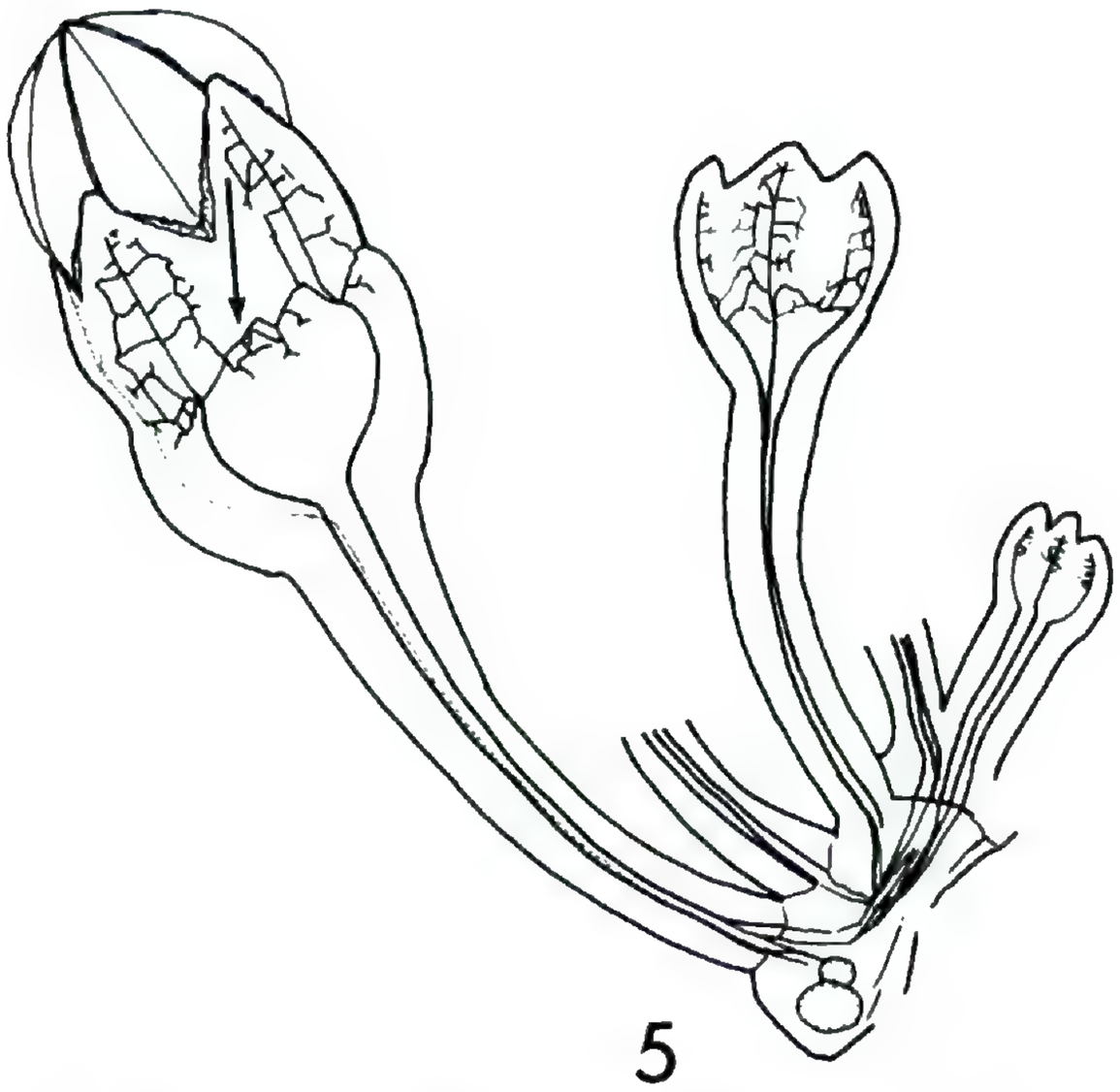
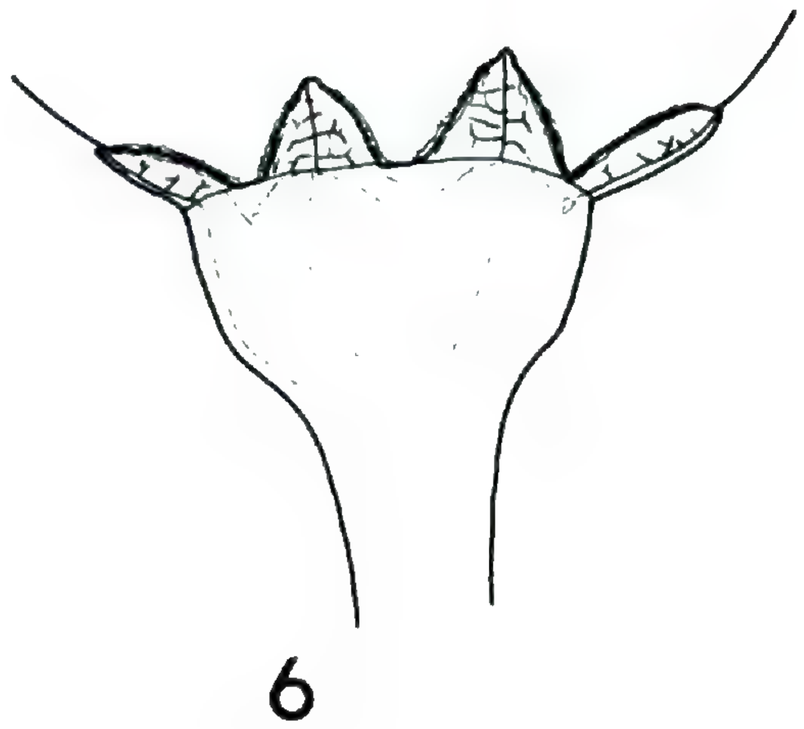


FIGURES 1–4. *Lycianthes maxonii* Standl. [After *D'Arcy 5507* (MO)].—1. Inflorescence with emerging buds. Calyx completely envelops the inner parts.—2. Corolla egresses from the calyx by stretching the apex into a thin sleeve. The teeth emerge beneath the sleeve area, and their vasculature moves out as they grow.—3. Corolla fully egressed and ready to open. The teeth have reached full size. The teeth enervated by the fused lateral veins are much smaller (see text).—4. Calyx in fruit showing intact sleeve and teeth.

THE GENERALIZED SOLANACEOUS CALYX

In many plant families, including the Solanaceae, the gamosepalous calyx consists of approximately five parts that are fused by their lateral margins to various levels, and the terms sepals and calyx lobes are often used interchangeably. Although the lobes may not in every case be homologous with the free sepals of the Archichlamidae, the studies of Copeland (1943) and Palser (1951, 1955) in the Ericaceae suggest that they are homologous in that family. In the Solanaceae examined in this study, the primary calyx vasculature consists of single traces running from the base of the pedicel to the tip of each lobe, differentiated even before the calyx lobes are evident as such. In cleared, stained whole material these traces maintain their identity throughout their length, although through the pedicel they are intimately associated and in serial sections they appear in this region as a siphonostele. Murray (1945) reported that in the Solanaceae gaps sometimes occur where the calyx traces leave the pedicel cylinder, but that this feature may vary even within a species. Techniques used in the present study did not distinguish parenchyma, and from the evidence seen of the vein architecture the presence of gaps could not be ascertained. The veins leading into the petals and those leading into the sepals were recognizably distinct from one another throughout their length, even in the relatively constricted base of the pedicel, and they apparently continue independently from the base of the pedicel to the top of the flower (Fig. 5). Connections between the two perianth whorls through exchange of sepal and petal traces were not indicated by Murray and in this study were found only as rare exceptions. The nature of connections between this vasculature of calyx and corolla in *Solanum boldoense* Dun. is discussed below. In one other instance, in only one of several flowers of an ornamental pepper (*D'Arcy 7001,* MO), a vein was seen running between the calyx and corolla near the base of only one of the sepals. The single trace entering the calyx lobes in the Solanaceae is in contrast to reports (Carlquist, 1961) for many other groups in which the sepals are supplied by three or more traces arising from the stele or stelar plexus but is similar to some genera of Ericaceae (Copeland, 1943; Palser 1951, 1955), which are slightly more specialized than the most primitive members of the family.



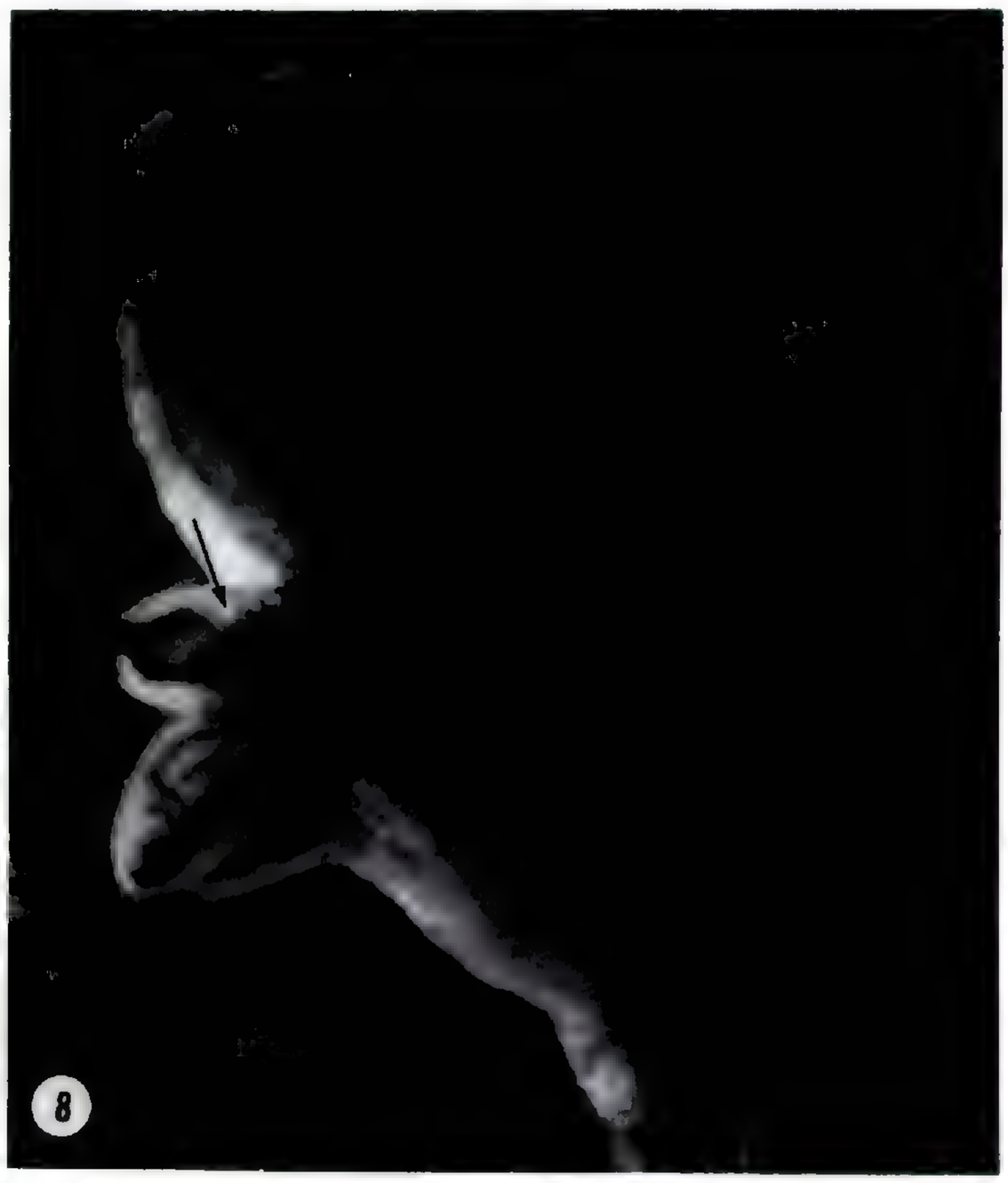


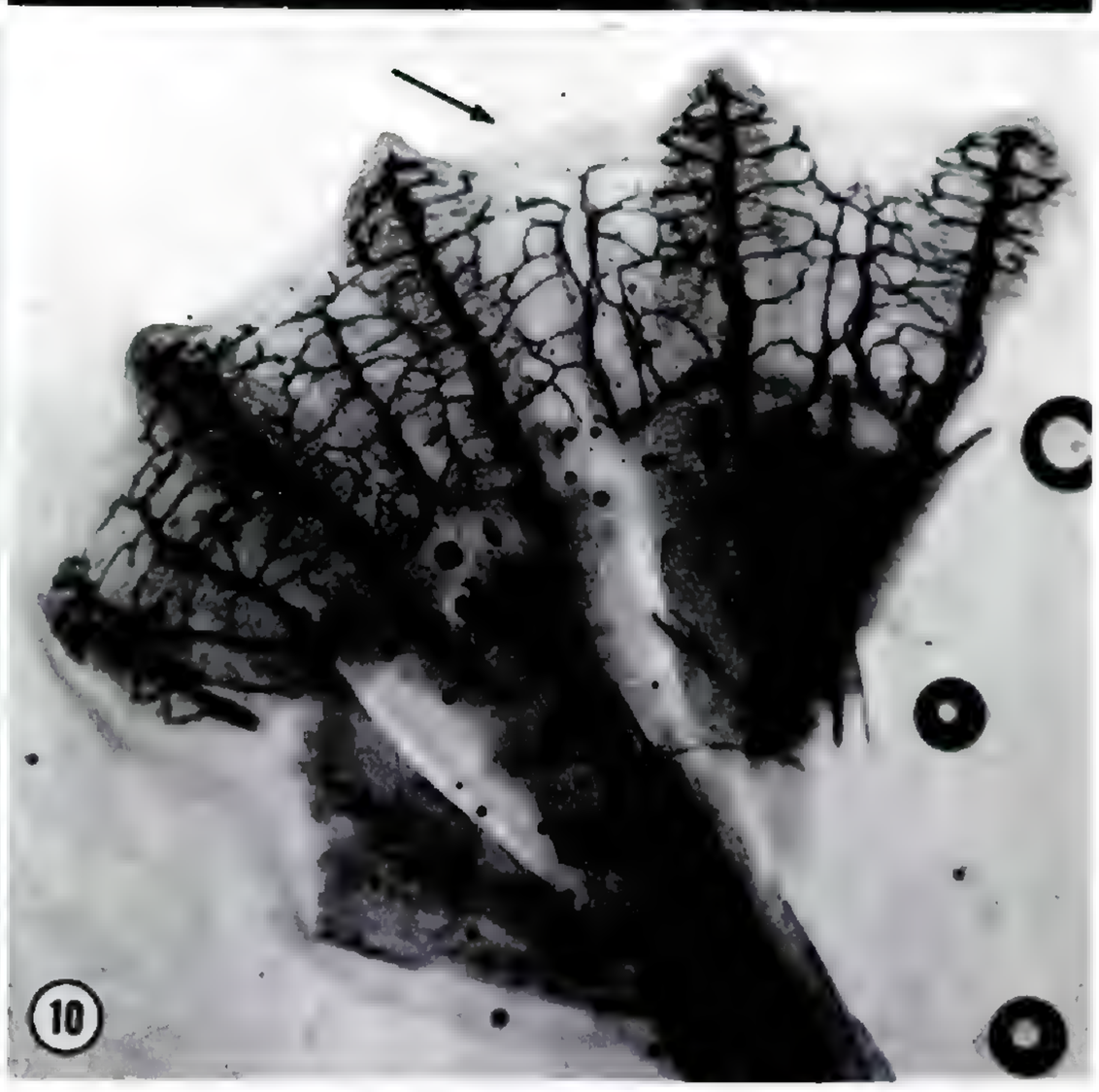
FIGURES 5, 6. *Solanum americanum* Mill. [After *D'Arcy 15159* (MO)].—5. Developing buds. Primary traces develop leaf-like minor lateral venation. Note calyx lobes splitting at the sutures and absence of vasculature in the suture area. Interconnector vein is at arrow.—6. Fruiting calyx with lobes split to the base.

Almost as soon as the calyx lobes are evident in the bud, a system of minor venation appears in each lobe that is usually soon oriented into two lateral veins flanking the midvein and a vein linking the basal, tangential portions of the laterals to form a prominent 'interconnector' vein (Figs. 5, 9). The interconnector may later assume structural importance in the fruiting calyx, as in the physaloid genera (*Physalis, Nicandra, Withania,* etc.). Other minor venation resembles that of a foliage leaf presenting a more or less acropetal, pinnate configuration on each side of the midvein (Figs. 5, 9). In her serial sections, Murray viewed the interconnector as anastomoses of the sepal traces, which at a slightly higher level broke into usually three separate veins. In the Solanaceae the interconnector often does not appear as such until after the minor venation has taken on its main outline, hence it is seen as secondary in an ontogenetic and perhaps phylogenetic sense. The pattern of a single sepal trace expanding into an interconnector and three major veins can be observed in other families such as the Boraginaceae, Scrophulariaceae, and *Cerastium* in the Caryophyllaceae. In many species of Boraginaceae there are two interconnectors, one at the base of the calyx and the other nearer the top, seemingly formed from venation displaced from the intermediate region by tight compression of the calyx around hard fruits.

Fusion of adjacent calyx lobes may involve ground tissue alone or both ground tissue and vasculature, and the level and nature of fusion may be usually of generic significance. Only one study is known that documents the developmental nature of calyx fusion in the Solanaceae. The fusion of ground tissue was investigated in *Datura* by Satina (1944), who used chimeras of different ploidy levels to show that in that genus the fusion of ground tissue is ontogenetic. The fusion takes place at a very early stage, and stages where fusion has not yet taken place cannot be identified by macroscopic methods. In many other genera of Solanaceae, from the time the flower bud is 1–3 mm long, there is little or no further alteration in length of the free sepal tips. From this it is assumed that by this stage the process of fusion is complete, but there is often a subsequent enlargement of the region of fusion.

After fusion of adjacent sepal margins, fusion of adjacent lateral sepal veins may take place, and the fusion is usually for most of the length of the longitudinal portions of the veins producing a second series of longitudinal veins alternate with the primary traces (Figs. 2, 4, 10). Such fusion is always the case in *Lycianthes* but appears only with irregularity in *Capsicum* (Fig. 10), often varying from sepal to sepal and from flower to flower. Fused laterals were put to taxonomic use by Waterfall (1958, 1967), Rydberg (1896), and others in the genus *Physalis,* in which groups of species were distinguished as being five-angled, 10-angled, or round, the condition mainly consequent on the state of fusion and development



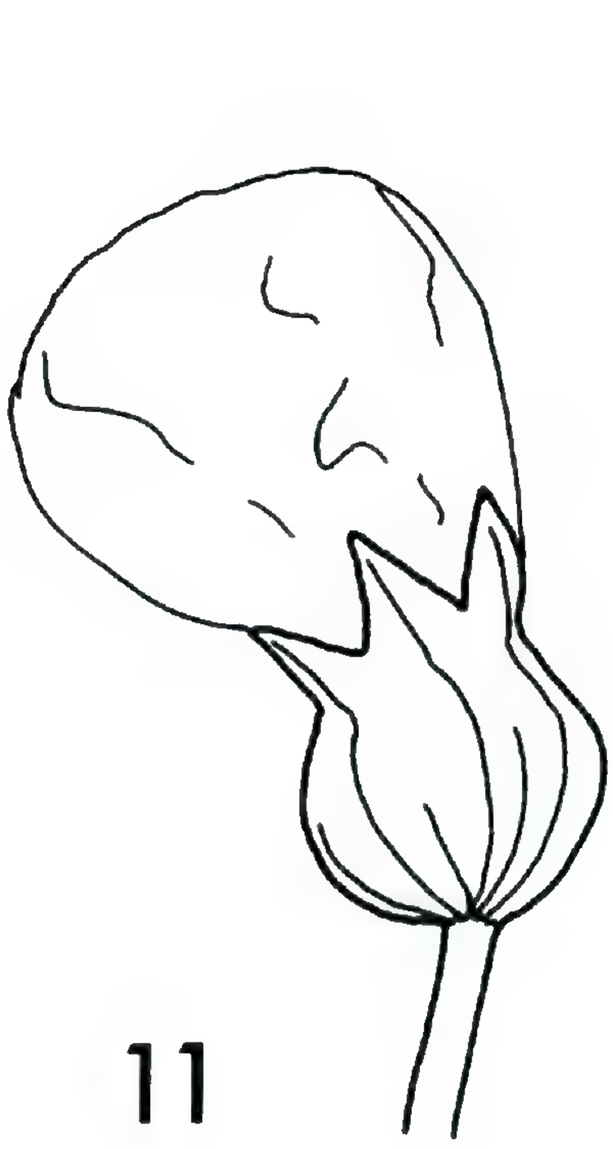


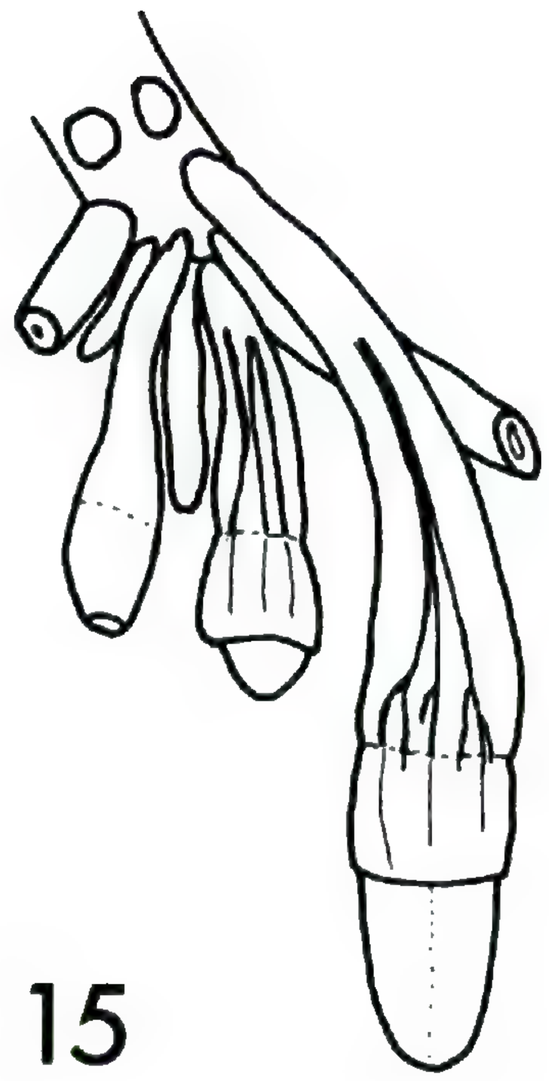
FIGURES 7–10. 7. Calyx of *Lycianthes maxonii* Standl. showing the reduced vasculature in the sleeve and the primary traces which have bent out within the teeth.—8. Calyx of *Lycianthes guianensis* (Dun.) Bitt. showing how the primary traces bend out within the teeth and the minor venation is directed basepetally as a result of this repositioning (arrow).—9. Calyx of *Solanum americanum* Mill. showing how the minor venation arising from the primary trace resembles the venation of a leaf. The interconnector can be seen at the arrow.—10. Calyx of *Capsicum annuum* L. opened to show the vasculature. The rudimentary sleeve can be seen at the apex between the reduced teeth (arrow). In this calyx the laterals have fused. It is speculated that the main teeth here are actually secondary teeth derived by outbending below the sleeve that have refused back against the primary traces (see text).

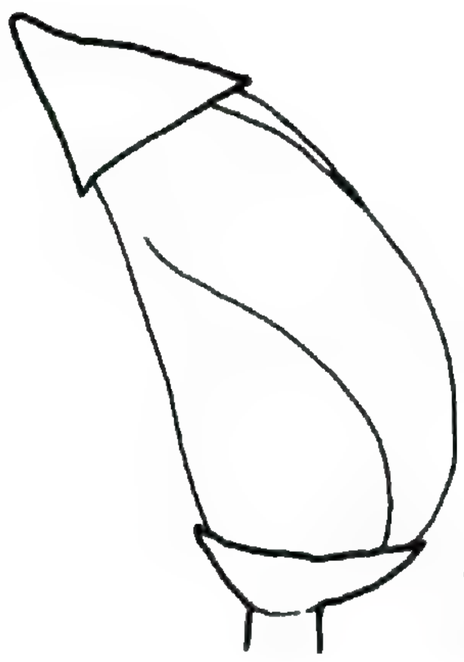
of the sepal laterals. Such fusion of apparently homologous laterals is common, and was observed to occur in the Phyrmaceae, in nearly all Lythraceae and Labiatae, common in the Caryophyllaceae (for example, *Cerastium*), but uncommon in the Scrophulariaceae.

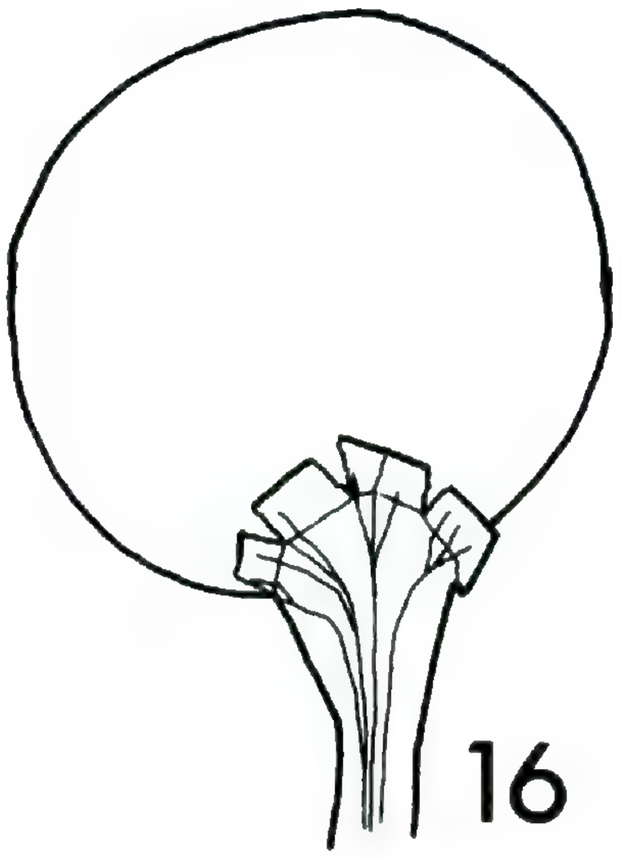
FLORAL EGRESS IN THE SOLANACEAE AND IN GENERAL

For the expansion of flowers in many families the corolla and often the stamens and stigma must find their way out of the enclosing outer









FIGURES 11–16. Modes by which floral egress from the calyx is achieved (examples).—11. Prefloral Egress: the flower egresses early and undergoes development and expansion outside the calyx (? *Margaranthus*).—12. Calyptrate Egress: the top of the calyx separates to leave the flower free to expand (*Magnolia*).—13. Distensive Egress: here the calyx stretches slightly to permit egress, but there is no marked distortion (*Anaemopaegma*).—14. Dehiscent Egress: in *Solanum*, only the tips of the calyx lobes are free in bud, but bigger lobes result from splitting at the sutures.—15. Distensive Egress: egress is by stretching of the distal portion of the calyx and a marked sleeve is produced (*Witheringia*).—16. Dehiscent Egress: *Witheringia* has distensive floral egress, but there is dehiscence for egress of the fruit.

perianth, which is usually the calyx. The mode of egress can be seen by observing the expansion of flowers in living material and often by observing dried herbarium specimens. In the flower with free sepals, egress of the corolla and other floral parts from the calyx is readily effected by outward movement of the sepals, but where there is fusion of the sepals, other arrangements may be necessary to permit egress of the pistil as it develops at anthesis and into fruit (Figs. 11–16). Where fusion of the calyx involves only the basal portion of the sepals, egress may involve no more than a slight stretching of the calyx without significant alteration of shape (Fig. 13). This is the case in many species of Verbenaceae (for example, *Clerodendrum splendens*), Polemoniaceae, Plantaginaceae, and other families, but in most Solanaceae there is high enough fusion that other mechanisms are invoked. Where fusion has progressed to unite upper portions of the sepals, egress may require either stretching and major distortion or tearing of the calyx at some point. In *Solanum* and *Lycopersicon* the sepals are usually fused except for their tips, and the sutures

or regions of fusion between them tear open in a valvate fashion to permit egress (Fig. 14). This is also found in *Symphytum* (Boraginaceae). The tearing may begin before the tip of the budding corolla reaches the length of the sepal tips or may be delayed until the corolla actually begins to unfold. Further tearing may take place with expansion of the fruit (Figs. 6, 16). In *Solanum, Lycopersicon,* and many other solanaceous genera, in which floral egress involves tearing at the sutures, there is no vasculature in the region of tearing. Where the calyx is fused to the top of the sepal tips as in *Lycianthes, Witheringia,* and *Anaemopaegma* and in many other Bignoniaceae, instead of by splitting, floral egress is achieved by stretching of the upper portion of the calyx (Fig. 13, 15). The stretched top portion of this calyx is manifestly thinner and smoother than the lower unstretched portion, and its appearance suggests that important stresses have been present as egress was effected. This area is the "sleeve" referred to above in the introductory description of the *Lycianthes* calyx. Not only is the surface sharply demarcated but the vasculature is much reduced or even absent in the stretched area. Where floral egress is by major stretching of this sort, possibilities for egress by splitting along the sutures of the calyx would be lessened by the presence of vasculature derived from lateral veins in the region between the primary calyx traces. Where sepals are fused to the top of the calyx leaving no opening, the calyx prefloration is termed complete. Here at least some tearing is necessary to create a circumference that can be stretched or to provide, by the tearing itself, a large enough opening for the floral parts to expand. Possibilities for splitting along the sutures is lessened by the presence of vasculature in this area; in genera such as *Solanum* and *Lycopersicon* in which egress is by splitting along the sutures, there is no vasculature or fusion of lateral veins in the suture area. Where there is fusion of laterals and hence vasculature in the suture areas, the tearing may continue down the calyx wall without regard to the position of vasculature. This sort of splitting without regard to the vasculature is a common situation, occurring in many genera with more advanced calyces: *Brugmansia, Bourreria pulchra* (Boraginaceae), *Silene* (Caryophyllaceae), *Tabebuia* (Bignoniaceae), etc. Where floral egress is by stretching, irregular splitting for egress of the fruit may also occur as in some species of *Witheringia* (Fig. 16). A special case of splitting without regard to the vasculature is the circumscissile or calyptrate dehiscence of the calyx in *Datura* and in *Eschscholzia* (Papaveraceae) and *Lundia* (Bignoniaceae). Species of *Margaranthus* (Fig. 11) and of *Salvia* (Labiatae) appear to undergo a prefloral egress in which the floral parts egress at an early stage and undergo much of their development outside the confines of the calyx. The above listed modes of floral egress are not exclusive categories, and variations occur that combine two or more of these methods. Thus in some species of *Cyphomandra* and in *Cordia polycephala* (Boraginaceae) prefloration of the calyx is complete except for a minute apical pore that may be stretched or split or both. In some species of *Magnolia* (Magnoliaceae) floral egress (from enclosing bracts instead of a true outer perianth) is achieved by calyptrate or longitudinal dehiscence or sometimes by both on the same flower (Fig. 12). Egress may not be necessary in some cleistogamous flowers, and in *Aristolochia* (Aristolochiaceae) the outer perianth expands into a corolloid structure with the androecium and gynoecium well enclosed during flowering. Mechanisms for egress of fruit are often related to systems of fruit dispersal. In the phys-

FIGURE 17. Stylized drawing of *Lycianthes* showing vasculature running into the teeth and then back to disappear in the sleeve.

aloid genera and in species of *Abutilon* (Malvaceae) and *Saccellium* (Boraginaceae), etc. the bladdery calyx may be a means of adapting a berry or achene-like fruit to wind dispersal. There are various stages from loosely investing calyces, as in *Physalis,* to tightly fitting calyces, as in *Trapa* and *Globularia* (stone fruits), *Solanum rostratum* (dry berry), and *Cordia sebestena* of the Boraginaceae (stone fruits). In the two last mentioned cases floral egress is by splitting and stretching, but the portal so formed does not enlarge, and the calyx and ovary are in snug contact for much of their development. Such a situation might logically preceed fusion of juxtaposed parts for the evolution of the inferior ovary in groups such as the Rubiaceae, Ericaceae, and Cucurbitaceae where the tissue surrounding the ovary is considered to be appendicular. "If epigyny in the Rubiaceae has a perigynous ancestry, there is no indication of it in the species alive today" (Cronquist, 1970), but if evolution proceeded from an enveloping calyx as suggested above, there was probably no need for perigyny as an intermediate stage. Although an inferior ovary usually avoids the need for egress of fruit, a variety of modes of floral egress can be seen in families with epigyny.

The Widespread Occurrence of Teeth

The calyx is often an enveloping structure made up of several pointed elements. These pointed elements can be viewed as teeth, a term used here for pointed structures accessory to a flower or inflorescence without regard to homology or derivation. It is necessary to emphasize the very widespread presence of such pointed structures in the architecture of inflorescences. In dicotyledons and monocotyledons alike the floral parts are regularly provided with a calyx terminating in one or more pointed elements, and where this is lacking an analogous form is often taken by pointed bracts or an awn. Such diverse groups as *Taxus, Ephedra, Najas, Saururus, Mirabilis,* and *Taraxacum* that lack toothed calyces have approximately similar structures derived from bracts. Teeth accompanying fertile parts are widespread and hence would seem to have important utility or selective value.

The Provision of Teeth in *Lycianthes*

Where fusion has proceeded along the entire length of the sepals and calyx prefloration is complete, the flower bud is no longer provided with teeth. Not surprisingly, some species that have lost their functional teeth in this way have evolved teeth that are not homologous with the teeth of an incompletely fused calyx. In species of *Lycianthes, Capsicum,* and *Witheringia* these nonhomologous or secondary teeth are produced around the side of the calyx and are often vascularized by outbending of the calyx venation at the points where they occur. Evidence of the nature of these secondary teeth is clear in the pattern of vasculature in many species. The primary calyx traces may arch outwards into the secondary teeth and return again to the calyx wall to end in the terminal or sleeve portion of the calyx. (Figs. 1–4, 7, 8, 17). In *Lycianthes* (Figs. 8, 17) the pinnate minor venation is consequently now directed downwards with respect to the form of the teeth but is still acropetal with respect to the traces it flanks and to the calyx as a whole. In different species, these secondary structures range from small lumps or umbos to elongate filiform teeth in some *Lycianthes* groups and to substantial acute teeth in *Capsicum chacoense.* In *Lycianthes* where the lateral sepal veins are fused to form a second series of vertically oriented veins, there is often a second series of secondary teeth vascularized by an outbending of the bases of the fused lateral veins. In some species of *Lycianthes, Capsicum,* or *Witheringia* in which outbending of the primary traces is slight, secondary teeth or umbos may not occur with regularity at each primary trace. Calyces of *Lycianthes rantonnei* may have from zero to ten teeth on different flowers on the same plant. Where the secondary teeth are small, they often shrink on drying and may be missed in casual viewing of herbarium material. Besides the solanaceous cases discussed here, what may be secondary teeth occur in at least a few other flowering plant groups such as *Lagerstroemia indica* (Lythraceae), *Hamelia* (Rubiaceae), and *Amphilophium* (Bignoniaceae).

Calyx Patterns in Some Related Genera

Cyphomandra. Adjacent laterals are not fused and sepals are fused to or near to the top of the calyx. Floral egress is by a combination of splitting and stretching.

Brachistus. The sepal tips are not fused and floral egress is achieved by small amounts of tearing and stretching. There are no evident swellings or ridges on the calyx wall, and there is no sleeve. It was partly on the basis of this primitive calyx

that D'Arcy et al. (1981) separated *Brachistus* from *Witheringia* and restricted it to three species.

Capsicum. In *Capsicum annuum* the minute sepal tips are free and floral egress is effected with minor stretching. Adjacent sepal laterals are usually close but usually not fused. The base of the calyx may develop a slight swelling and outbending of the vasculature from its otherwise cylindrical structure. *Capsicum chinense* has a conspicuous but unvascularized swelling or ferrule where the pedicel flares into the receptacle or calyx base. *Capsicum chacoense* and *C. baccatum* have well-developed secondary teeth, which appear externally like ordinary free sepal tips, but clearing of the tissue reveals that these teeth are secondary, and the primary vasculature runs first to the tip of the teeth and then back down to the calyx and into the sleeve. The basipetal minor venation seen in the teeth of species of *Lycianthes* was not seen in *Capsicum chacoense.* The sleeve in *Capsicum* is inconspicuous.

Jaltomata. The bud of *J. procumbens* is a flat-topped cylinder. The calyx lobes are coherent for their full length, there are no discernible free tips, and prefloration is apparently complete. The lateral sepal veins are fused as far as the rim of the flat bud, while along both the primary sepal traces and the fused laterals, ridges run from the base of the receptacle to the rim of the bud. These ridges are suggestive of incipient teeth or umbos in the manner of the secondary teeth of *Lycianthes.*

Lycianthes. Adjacent laterals are always fused and floral egress is effected by stretching of the calyx rim, which produces a recognizable sleeve. There is a tendency for the development of secondary teeth from the side or base of the calyx wall and for these to be vascularized by outbending of the primary sepal traces and the longitudinal portions of the fused laterals.

Lycopersicon. Calyces are like those in *Solanum,* but the free sepal tips are proportionately longer.

Margaranthus. The calyx is like that in *Physalis* but splitting is very short. Much of floral development seems to take place after egress has been initiated, and this prefloral egress can be used for routine separation of the similar *Physalis lobata* Nutt.

Nicandra. Prefloration is complete and floral egress is effected by splitting at the sutures. The interconnector becomes lignified in the accrescent calyx. Two well-spaced laterals appear on each side of the sepal midvein.

Physalis. Prefloration is like that in *Solanum,* and floral egress is by longitudinal splitting at the sutures. Adjacent laterals are mostly fused, but in some species there are two pairs of laterals as in *Nicandra.* The interconnector usually becomes lignified in the accrescent fruiting stage.

Solanum. Adjacent calyx teeth are fused partway up, but there is no fusion of lateral veins except for the interconnector. Floral egress is by splitting at the unvascularized sutures. In some cases there is further splitting in fruit. Exceptions are discussed below.

Witheringia. There is no fusion of adjacent laterals, and floral egress is achieved by stretching, often producing a distinct sleeve. In some species there are umbos at the base of the calyx, and in fruit these species may be difficult to distinguish from species of *Lycianthes.* Some species split for egress of fruit. This calyx appears to be highly evolved in contrast to the primitive calyx in *Brachistus.*

SOME SPECIALIZED EXCEPTIONS IN SOLANUM

In *Solanum seaforthianum* floral egress combines some splitting with stretching, and there are no other apparent deviations from the normal pattern. But in the closely related *S. boldoense* of Cuba (Fig. 19) the base of the calyx is expanded into a conspicuous cupule or ferrule, and there is a reticulum of fine venation extending below the connector, which appears to be supplied by traces from both the corolla and the calyx. *Solanum surinamense* Steud. (Fig. 8) has a fine reticulum like the two species just mentioned and five prominent apical unvascularized lobes. These three exceptions have floral egress by stretching. Other species with prominent basal cupules, *S. hazenii* and *S. antillarum,* have no departures from the normal *Solanum* calyx vasculature.

LYCIANTHES AS A GENUS

A distinctive feature of plants assigned to *Lycianthes* is the structure of the calyx. This calyx is quite different from the calyx of *Solanum* and is more like that of species of *Capsicum* and *Witheringia.* Although a few species of *Solanum* seem to approach *Lycianthes* in the manner of portal opening, they are not good candidates for consideration as intermediates between *Solanum* and *Lycianthes.* The calyx in *Solanum* with

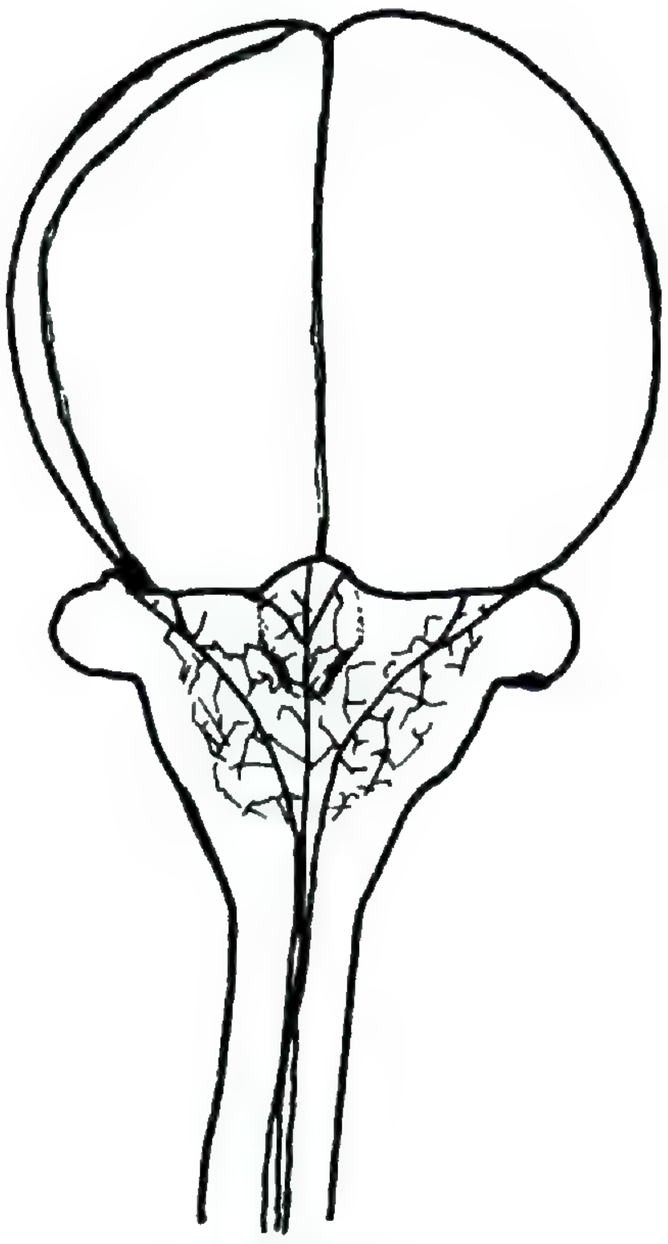


FIGURE 18. The exceptional calyx vasculature of *Solanum surinamense* Steud. Note the proliferation of minor venation below the unvasculaturized teeth.

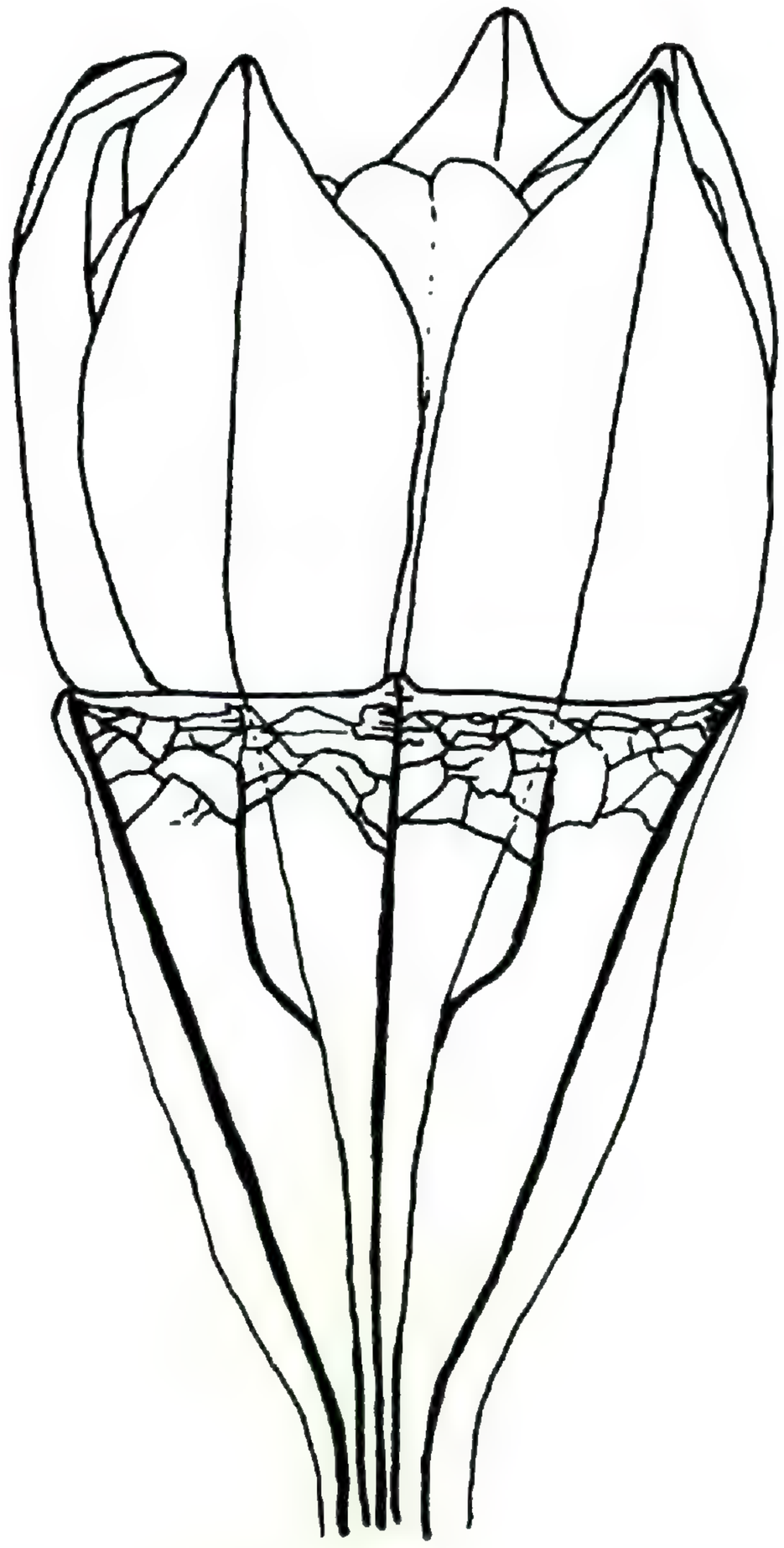


FIGURE 19. The exceptional calyx vasculature of *Solanum boldoense*. Note connection between calyx and corolla traces.

its less complicated vasculature should probably be considered primitive among the genera listed above and that of *Lycianthes* to be much more advanced.

Other characters separating *Lycianthes* are generally inconclusive. Chromosomes, wood histology, and pollen have provided little assistance. The stone cells invoked by Bitter (1919) occur in other genera and also in *Solanum*. Reduced inflorescences, entire leaves, and spinelessness are useful but are not generic characters. Perhaps improved chemical information will provide better demarcation. There may nevertheless be some important biological differences: there are few specimens in herbaria (Nee, 1981; Symon, 1986) and many of the species flower nocturnally (Nee, 1981).

Although clearly distinguished only by its calyx, this character indicates a significant advance in the evolution of at least one floral organ over the less specialized genus *Solanum*. From a practical point of view, it is useful to consider the more than one hundred species of this advanced group as a generic entity with its own name. This is helpful in gaining accessibility to the literature and to specimens filed in herbaria. Species of this group are with few exceptions easily identifiable by a glance at the calyx, and confusion in dealing with these exceptions generally relates to their similarity to *Witheringia* or *Capsicum* and not to *Solanum*. The diagnostic presence of a sleeve and the frequent presence of ten lateral teeth in two series distinguish it readily from *Solanum*.

THE CALYX IN PHYLOGENY AND TAXONOMY

Studies in the Lauraceae (Kasapligil, 1951), Ranunculaceae (Tepfer, 1953), and other primitive families, usually with distinct sepals, generally show that the sepals are vascularized by a series of traces oriented in much the same way as the traces in leaves of the same plant (see Esau, 1960, 1965). The work of Copeland (1943) and Palser (1951, 1955) in the Ericales lends support to the view that the calyx lobes in the Sympetalae are homologous with those of the more primitive families. Their work outlines a sequence of calyx evolution that parallels the trends in specialization of other organs in those plants. The sequence of evolution of primary calyx vasculature in the

Ericales may be summarized as follows (sepals are usually five):

1. Three independent traces per sepal (15 gaps) (*Befaria, Leucothoe racemosa,* etc.).
2. Three traces per sepal (ten gaps): median plus laterals derived from an intermediate sepallary trace common to two sepals (*Chamaedaphne*).

3a. One trace per sepal that soon divides into a median and two laterals (five gaps) (*Elliottia, Gaultheria, Ledum,* etc.).

3b. Three traces per sepal (five gaps): median plus laterals derived from intermediate petal bundles (*Kalmia, Pyrola, Clethra,* etc.).

4. One trace per sepal (five gaps): no laterals (*Cassiope mertensiana*).

In the Ericales these branching patterns occur in the receptacles, and at the level of sepal expansion the laterals may branch into five to nine veins. From stage 2, there is the possibility of advancement to either stage 3a or 3b.

In the genera of Solanaceae here examined, the primary calyx vasculature is all at stage 3a, but at higher levels in the calyx, the vasculature shows two developments not seen in the Ericales: fusion of sepal laterals and enervation of secondary teeth or appendages. Fusion of calyx parts has opened new possibilities for evolution of vasculature. The degrees of calyx fusion and possibilities for egress are categorized in Table 1.

TABLE 1. Degrees of calyx fusion and possibilities for egress.

Perianth Structure	Level of Advancement	Mode of Egress
Outer perianth wanting	1.	No confinement
Outer perianth of free segments (sepals)	1.	No confinement
Outer perianth fused to near the base	2.	Expansion
	3.	Stretching
Outer perianth mostly fused, tips free	3.	Stretching
	4.	Splitting at sutures
Outer perianth fused to the top	4.	Splitting at sutures
	5.	Tearing irrespective of sutures
	6.	Circumscissile tearing
Special situations	7.	Prefloral egress
	8.	Cleistogamy

ADVANCES AND REVERSALS OF CALYX EVOLUTION

One may envision a sequence of evolutionary steps that would yield a condition so like the starting point that the advancement that had occurred in between would not be detected. Such a sequence may have taken place in *Capsicum.* It is probable that the calyx of *Capsicum chacoense* evolved from a primitive stage such as one sees in *Solanum* to its present form by a sequence like that in *Lycianthes.* If the secondary teeth were not of selective value under new environmental conditions they might become fused back into the calyx wall and sleeve. And if the sleeve was not of selective value it might disappear. Then there would be a rudimentary sleeve, and the formerly outbent vasculature of the secondary teeth would be juxtaposed radially against the primary trace and would tend to fuse with it. There would remain a rudimentary sleeve and probably small teeth, which would be the fusion product of the secondary teeth and the primary traces, these being all that was left of the primary (in the sense of *Solanum*) teeth. If this were the case, could it be detected? Such a series may well have taken place in *Capsicum annuum* and other species that have calyces with reduced teeth, inconspicuous sleeves, and floral egress by stretching (Fig. 10). Thus the sequence hypothesized here, although supported only by intuition, calls for considerable caution in extrapolating evolutionary sequences to other groups. Another likelihood is that an evolutionary sequence like that outlined for *Lycianthes* has taken place in other groups and has provided the stage for evolution of structures still more advanced. Thus in the Bignoniaceae, *Amphilophium* has a well-defined sleeve not unlike that of *Lycianthes*—this should probably not be considered unique in the family, but rather an indication that other members of the family also have evolved elaborate calyx structure that cannot be readily assessed or understood on the basis of present calyces. The sleeve and secondary teeth of *Lycianthes* should probably not be regarded as unique evolutionary etudes or as phylogenetic endpoints but as stages on a larger development route travelled by many advanced plant groups.

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SEROTAXONOMY OF *SOLANUM, CAPSICUM, DUNALIA,* AND OTHER SELECTED SOLANACEAE[1,2]

RICHARD N. LESTER[3] AND PHILIP A. ROBERTS[4]

ABSTRACT

Serotaxonomic comparisons were made on about 50 species of Solanaceae. Immunoabsorption data were obtained from reactions of seed protein antigen systems with antibody systems absorbed by several antigen systems in numerous permutations. Relationships of the taxa were computed by newly developed methods. Twenty species of *Solanum,* mostly of subg. *Leptostemonum,* were compared using six antisera. *Solanum nigrum* (subg. *Solanum*) was serologically distinct from the others. Several groups of species belonging to different sections of *Solanum* were recognized. Phenetic and phyletic relationships within sect. *Androceras* were explored. Re-analysis of a complete cubic matrix of immunoabsorption data for eight species of *Solanum* rearranged relationships slightly but emphasized the divergence between different sections of this genus. A broad survey was made using an antibody system raised to *Capsicum annuum.* This revealed the distinctiveness of *Nicandra* from other Solanaceae, several possible inter-generic relationships, but also some unlikely ones. Further studies revealed closer relationships of *Dunalia* species to *Capsicum* than to *Iochroma.*

Protein characters are valuable in plant taxonomy for assessing inter-generic and even inter-family relationships (Jensen & Fairbrothers, 1983). Within the Solanaceae several serological studies have been made by workers such as Chester, Hammond, Tucker, Gray, and Lester (see review by Lester, 1979).

Because of the complex physico-chemical properties of proteins, and the even more complex phenomena of immunological reactions, many different serotaxonomic techniques have been developed (Jensen & Fairbrothers, 1983). Immunoabsorption resolves subsets of antigenic determinant sites as recognized by corresponding subsets of antibodies after the removal of common antibodies from the antibody system by absorption by other antigen systems. Recent developments in the theoretical and practical aspects of immunoabsorption techniques and the analysis of the resultant data by appropriate numerical taxonomic procedures have been discussed in detail (Lester, 1979; Lester et al., 1983). For this paper these procedures were applied to selected species of Solanaceae.

MATERIALS AND METHODS

Seed samples from the Birmingham University Solanaceae Collection (Tables 1–3) were used to prepare protein extracts, to induce antibody production in rabbits, and for subsequent immunological experiments using absorbed antibody systems. Procedures, especially the scoring and analysis of results, followed those described by Lester (1979) and Lester et al. (1983).

Three sets of experiments were conducted.

1. Twenty accessions of *Solanum,* mostly of subg. *Leptostemonum* (Table 1) were compared using six antibody systems (data published in Lester et al., 1983).
2. Eight species from diverse sections of the genus *Solanum* (Table 2) were compared using eight antibody systems (data published in Lester, 1979).
3. About 25 species of *Capsicum, Solanum,* and other genera of Solanaceae, mostly of tribe Solaneae (Table 3) were compared using one antibody system (Lester, unpubl. data).

Most of these data have now been analyzed by most of the procedures described by Lester et al. (1983), especially by using Jaccard's and similar coefficients to estimate phenetic relationships. Some of the data sets also were subjected to cladistic analysis. Many dendrograms were produced by different analyses of the various sets and subsets of data, some of which are presented herein (Figs. 1–6).

[1] We are grateful to Sarah Marsh for growing these plants, to the Science and Engineering Research Council (U.K.) for financial support, and to Julie Brean, Barbara Klauza, and Sarah Sutton for technical assistance.

[2] This paper was part of the Second International Symposium of the Biology and Systematics of the Solanaceae presented at the Missouri Botanical Garden on 3–6 August 1982.

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TABLE 1. Listing and classification of the 20 accessions of *Solanum* species that were compared immunologically using antibody systems to CAP, ROS, SIS, QUT, TOR, and PRN.

Taxa	Code	Acc. No.
Subg. *Leptostemonum* (Dun.) Bitt.		
Sect. *Acanthophora* Dun.		
S. capsicoides All.	CAP	S.0866
S. chloropetalum Schl.	CHL	S.0021
S. viarum Dun.	VIA	S.1418
Sect. *Androceras* (Nutt.) Bitt. ex M.		
Ser. *Androceras*		
S. rostratum Dun.	ROS	S.0097
	ROS	S.0399
S. fructo-tecto Cav.	FTO	S.0025
Ser. *Violaceiflorum* Whalen		
S. heterodoxum Dun.	HET	S.0593
S. citrullifolium A. Br.	CIT	S.0195
	CIT	S.0127
Sect. *Cryptocarpum* Dun.		
S. sisymbriifolium Lam.	SIS	S.1099
	SIS	S.0136
Sect. *Lasiocarpa* (Dun.) D'Arcy		
S. hirtum Vahl	HIR	S.1142
S. quitoense Lam.	QUT	S.0972
S. tequilense A. Gray	TEQ	S.0973
Sect. *Oliganthes* (Dun.) Bitt.		
S. anguivi Lam.	ANG	S.1335
S. prinophyllum Dun.	PRN	S.0386
	PRN	S.1444
Sect. *Torva* Nees		
S. hispidum Pers.	HIS	S.0017
S. torvum Swartz	TOR	S.0839
Subg. *Solanum*		
Sect. *Solanum*		
S. nigrum L.	NIG	S.0498

TABLE 3. List of accessions of *Capsicum, Dunalia,* and other genera of Solanaceae that were compared immunologically using antibody system to *Capsicum annuum.*

Code	Acc. No.	Taxa
ATHEN PIC	S.1069	*Athenaea picta*
ATROP BEL	S.0077	*Atropa belladonna*
CAPSI ANN	S.1083	*Capsicum annuum*
CAPSI BAC	S.0749	*C. baccatum*
CAPSI CHA	S.0750	*C. chacoense*
CYPHO BET	S.0045	*Cyphomandra betacea*
DATUR STR	S.0185	*Datura stramonium*
DUNAL AUS	S.0379	*Dunalia australis*
DUNAL BRE	S.0375	*D. breviflora*
DUNAL BRF	S.0377	*D. breviflora*
DUNAL LOR	S.0376	*D. lorentzii*
DUNAL TUB	S.1094	*D. tubulosa*
HYOSC NIG	S.0289	*Hyoscyamus niger*
IOCHR SPE	S.1599	*Iochroma* sp.
IOCHR UMB	S.1602	*I. umbrosa*
LYCIU CES	S.0368	*Lycium cestroides*
LYCOP ESC	S.1152	*Lycopersicon esculentum*
NICAN PHY	S.0082	*Nicandra physalodes*
NICOT TAB	S.0329	*Nicotiana tabacum*
PHYSA ANG	S.0512	*Physalis angulata*
SALPI ORI	S.0159	*Salpichroa origanifolia*
SARAC UMB	S.0117	*Saracha umbellata*
SCOPO LUR	S.0104	*Scopolia lurida*
SOLAN AET	S.0156	*Solanum aethiopicum*
SOLAN CAP	S.0263	*S. capsicastrum*
TRECH SAT	S.0234	*Trechonaetes sativa*
WITHA SOM	S.0242	*Withania somnifera*
WITHE COC	S.1582	*Witheringia coccoloboides*

TABLE 2. List of eight species of *Solanum* that were compared immunologically using antibody systems to all eight species.

Code	Acc. No.	Species	Section
TUBERO	S.0952	*S. tuberosum* L.	*Petota*
SCABRU	S.0243	*S. scabrum* Mill.	*Solanum*
MAURIT	S.0049	*S. mauritianum* Scop.	*Brevantherum*
HENDER	S.0167	*S.* ×*hendersonii* Hort.	*Pseudocapsicum*
SEAFOR	S.0051	*S. seaforthianum* Andr.	*Jasminosolanum*
AETHIO	S.0279	*S. aethiopicum* L.	*Oliganthes*
SIMILE	S.0211	*S. simile* F. Muell.	*Archaesolanum*
CITRUL	S.0168	*S. citrullifolium* A. Br.	*Androceras*

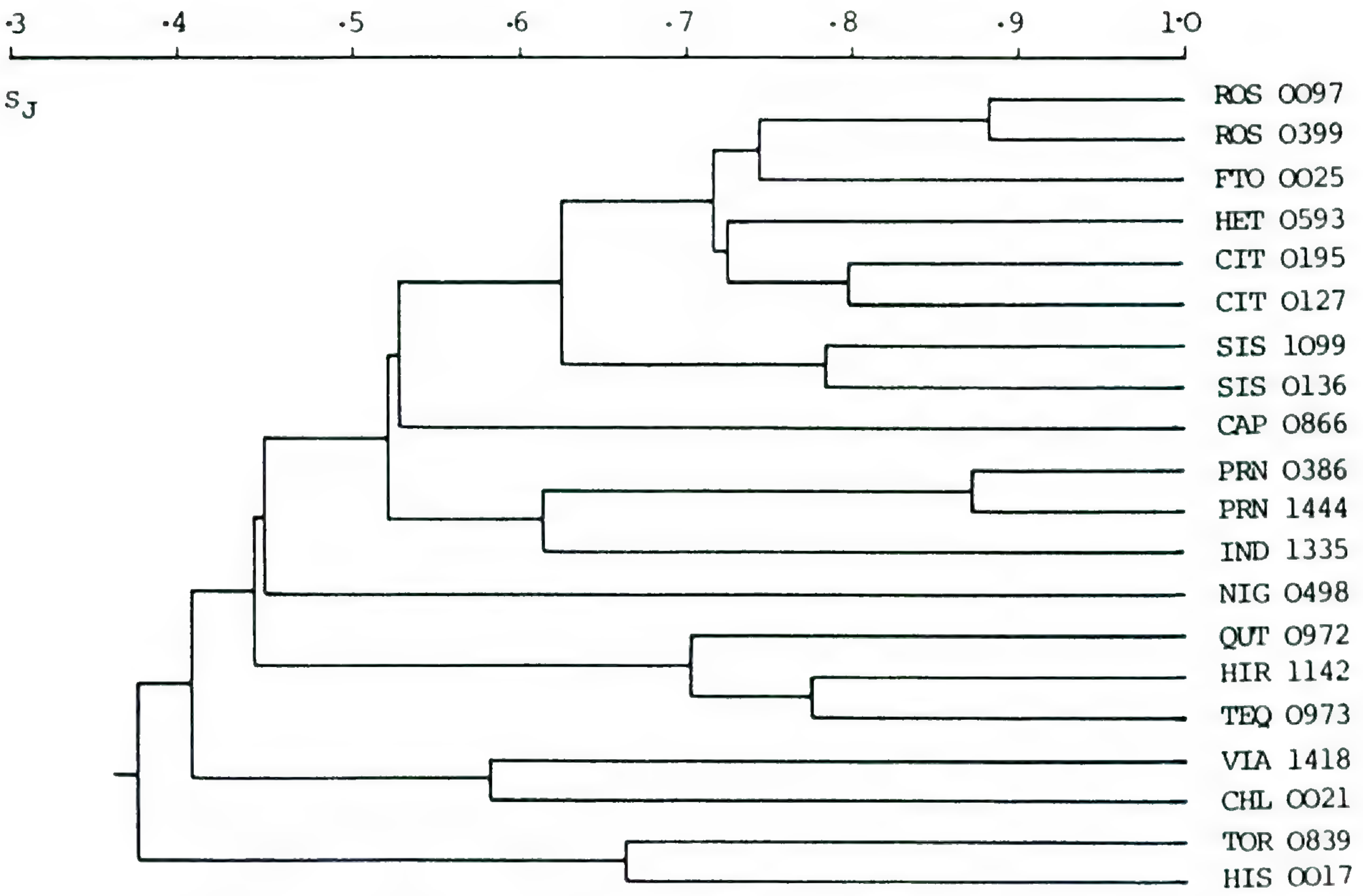

FIGURE 1. Phenogram of immunological similarities of 20 accessions of *Solanum* species calculated by Jaccard's coefficient and group average clustering (for explanation see text and Table 1).

RESULTS AND DISCUSSION

SOLANUM SUBG. *LEPTOSTEMONUM*

This set of data has already been described and analyzed in several ways (Lester et al., 1983): Jaccard's coefficient and group average clustering is justified on theoretical grounds and produces a taxonomically acceptable phenogram (Fig. 1).

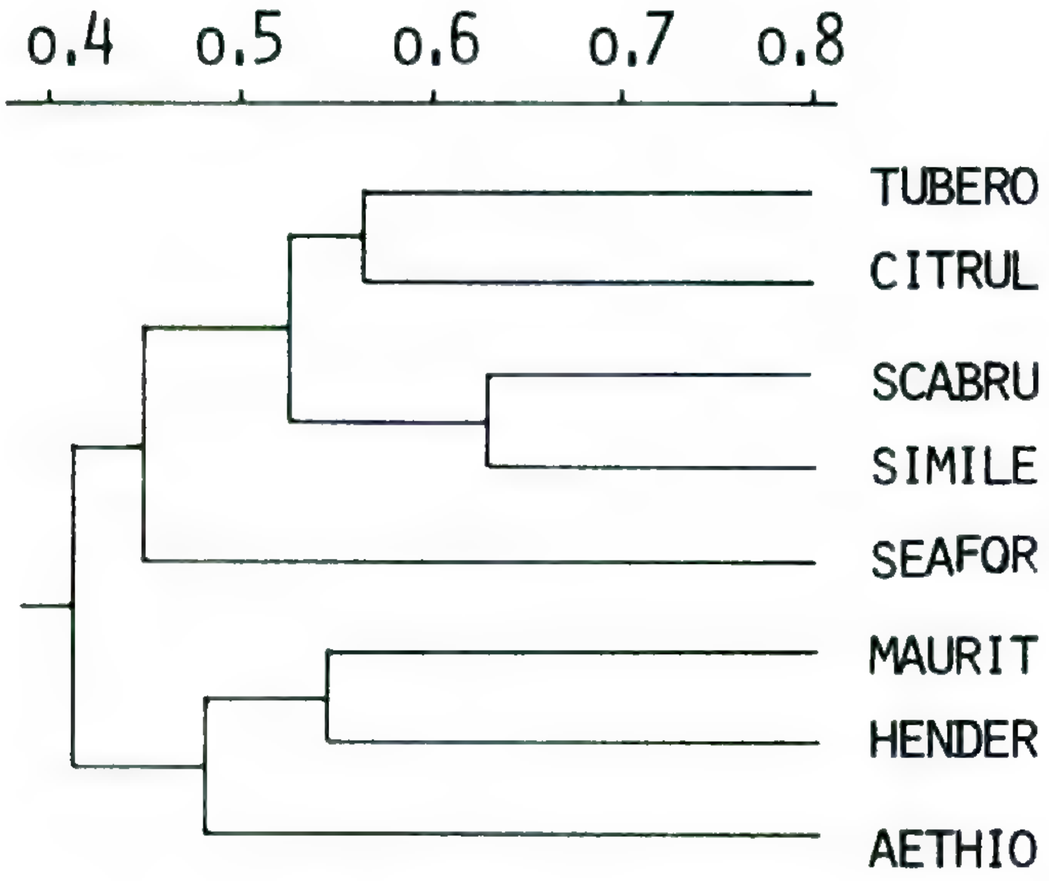

FIGURE 2. Phenogram of immunological similarities of eight *Solanum* species calculated by Jaccard's coefficient and group average clustering (for explanation see text and Table 2).

Solanum nigrum showed little similarity to the other species, which supports the major taxonomic distinction between subg. *Solanum* and subg. *Leptostemonum*. *Solanum torvum* and *S. hispidum* of sect. *Torvaria* were grouped together but were well separated from any other taxa. *Solanum hirsutum, S. tequilense,* and *S. quitoense,* members of the distinctive sect. *Lasiocarpa,* were grouped together and separated from other taxa. *Solanum chloropetalum* and *S. viarum,* two morphologically similar and partly interfertile species of sect. *Acanthophora,* were grouped together. *Solanum capsicoides,* of the same section, was placed some distance away, but the antigen system of this species produced nonspecific reactions.

The two accessions of *Solanum prinophyllum* from Australia were placed together and were joined at a low level by *S. anguivi* from Africa, which is also classified in sect. *Oliganthes.*

The two accessions of *Solanum sisymbriifolium,* sect. *Protocryptocarpum,* were placed together and were linked with members of sect. *Androceras.* Two accessions of *S. citrullifolium* were joined by *S. heterodoxum,* also of ser. *Violaceiflorum,* and two accessions of *S. rostratum* were joined by *S. fructo-tecto,* also of ser. *Androceras.*

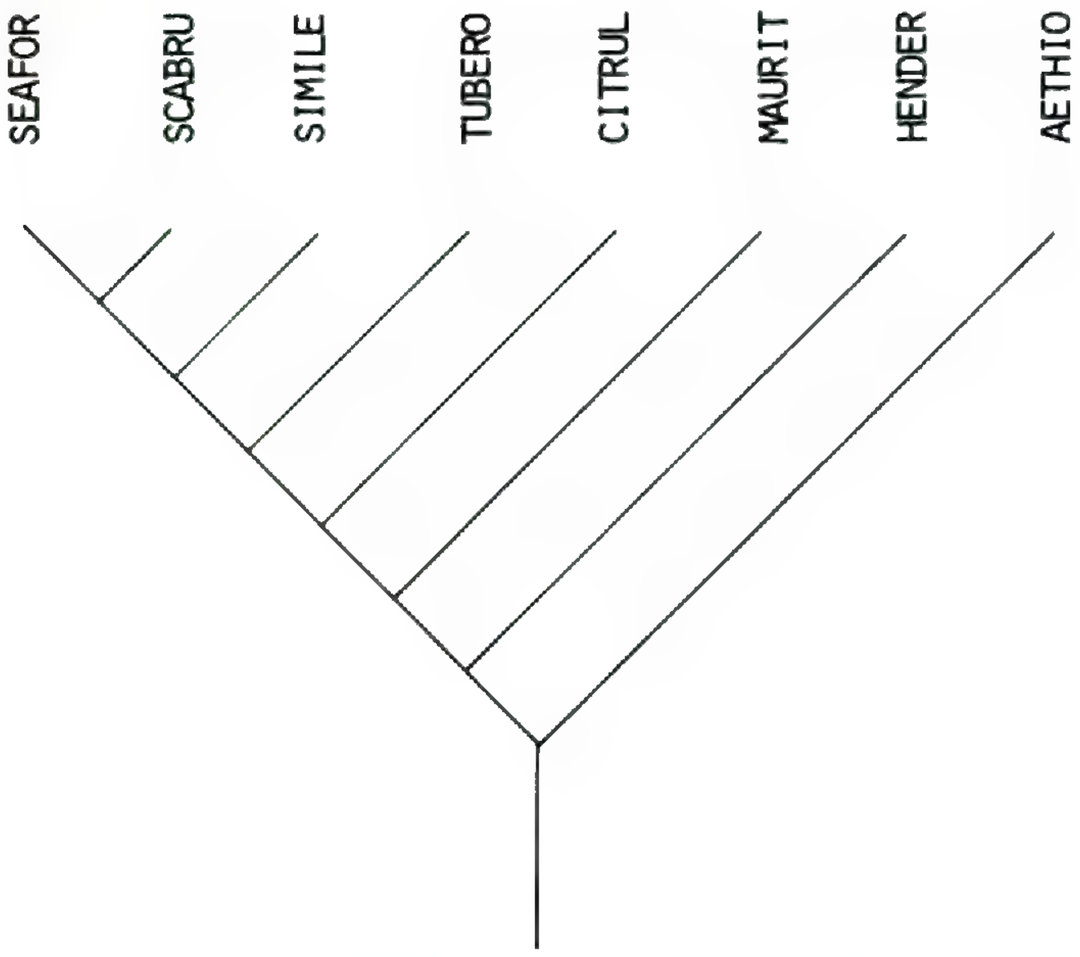

FIGURE 3. Cladogram of eight species of *Solanum* derived from immunological data by the Dollo method (for explanation see text and Table 2).

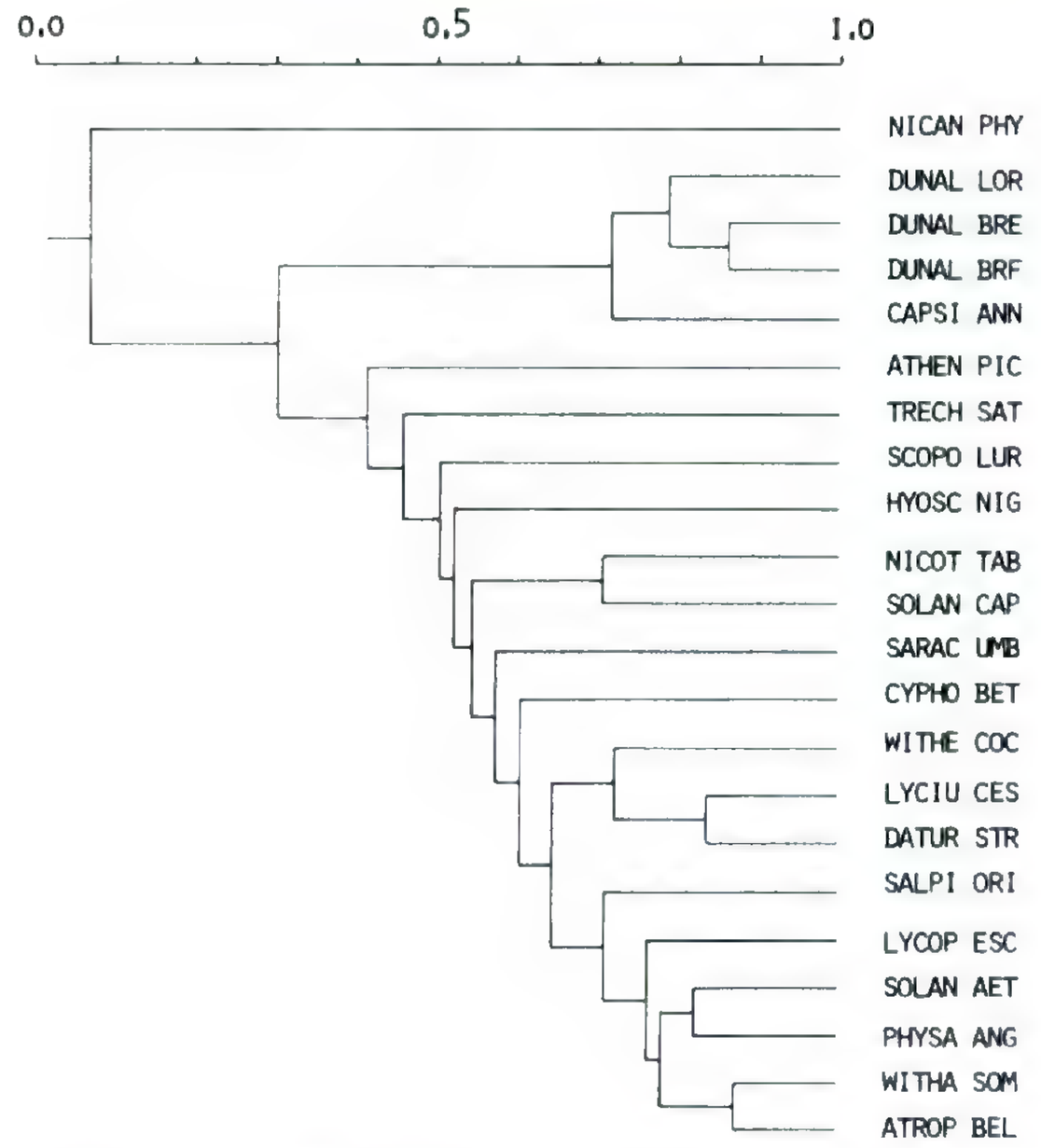

FIGURE 4. Phenogram of immunological similarities of 22 accessions of various genera of Solanaceae calculated by Jaccard's coefficient and group average clustering (for explanation see text and Table 3).

Nearly all of these serologically indicated relationships made good taxonomic sense, but in most cases the various sections of *Solanum* are very distinct and there is little information on the affinities between them.

An essay at cladistic analysis (Lester et al., 1983) using only data from the antibody system to *S. rostratum* suggested an evolutionary sequence (with distances between evolutionary units as indicated in parentheses): ancestor (17), SIS S.0136, SIS S.1099, (6) HET S.0593 (3) CIT S.0127, (3) CIT S.0195, (5) FTO S.0025 (4) ROS S.0097, ROS S.0399. This is a progression from *S. sisymbriifolium,* a perennial plant with actinomorphic violet flowers and red berries, through to *S. rostratum,* a normally short-lived annual plant with strongly zygomorphic yellow flowers and dry capsules. In each morphological attribute an evolutionary sequence can be recognized going from *S. sisymbriifolium,* through *S. heterodoxum, S. citrullifolium* and *S. fructo-tecto* to *S. rostratum.* These conclusions are the converse of Whalen's (1979) evolutionary scheme, but are supported by spermoderm studies (Lester, unpubl. data).

Other cladograms, produced from these immuno-absorption data, were published by Lester et al. (1983). One cladogram had successive simple branches to *S. quitoense, S. torvum, S. capsicoides, S. prinophyllum,* and finally *S. sisymbriifolium* and *S. rostratum.*

Cladistic analysis of the total data set was made by computer using the Dollo and Wagner methods (Felsenstein, 1982), but the results are not presented here because the data were analyzed in only one sequence and the resultant cladograms were not taxonomically acceptable.

EIGHT DIVERSE SECTIONS OF *SOLANUM*

This set of data was described and analyzed in an elementary way in Lester (1979). Re-analysis, using the preferred Jaccard's coefficient and group average clustering, provided a new dendrogram (Fig. 2).

Some taxonomic groupings are maintained, such as those of *Solanum scabrum* and *S. simile* (sects. *Solanum* and *Archaesolanum*) and *S. hendersoni, S. mauritianum,* and *S. aethiopicum* (sects. *Pseudocapsicum, Brevantherum,* and *Oliganthes*), but *S. citrullifolium* (sect. *Androceras*) is now grouped with *S. tuberosum* (sect. *Petota*), which is unacceptable on morphological grounds. *Solanum seaforthianum* (sect. *Jasminosolanum*) links with the rest at a very low level. The taxonomic relationships between these sections have been discussed previously (Lester, 1979). In general these results suggest that most of these sections of the genus *Solanum* are diverse and are not closely related to each other. In such a situation, different procedures of analysis can produce radically different dendrograms. The inclusion of many more species, even without using any more antibody systems, would improve the taxonomic information and the stability of the classifications.

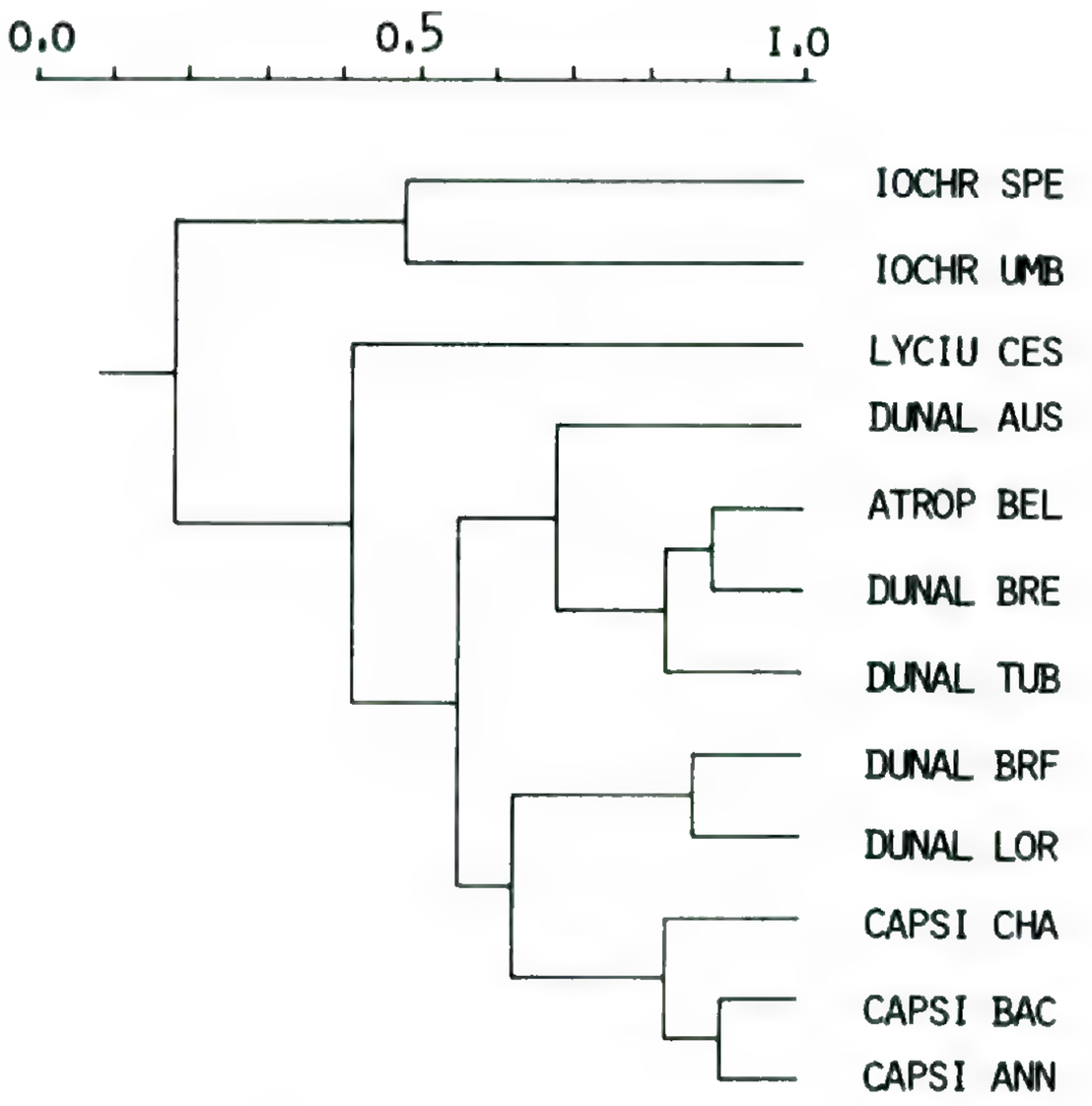

FIGURE 5. Phenogram of immunological similarities of 12 accessions of *Capsicum, Dunalia,* and other genera calculated by similarity ratio (coeff. no. 28) and group average clustering (for explanation see text and Table 3).

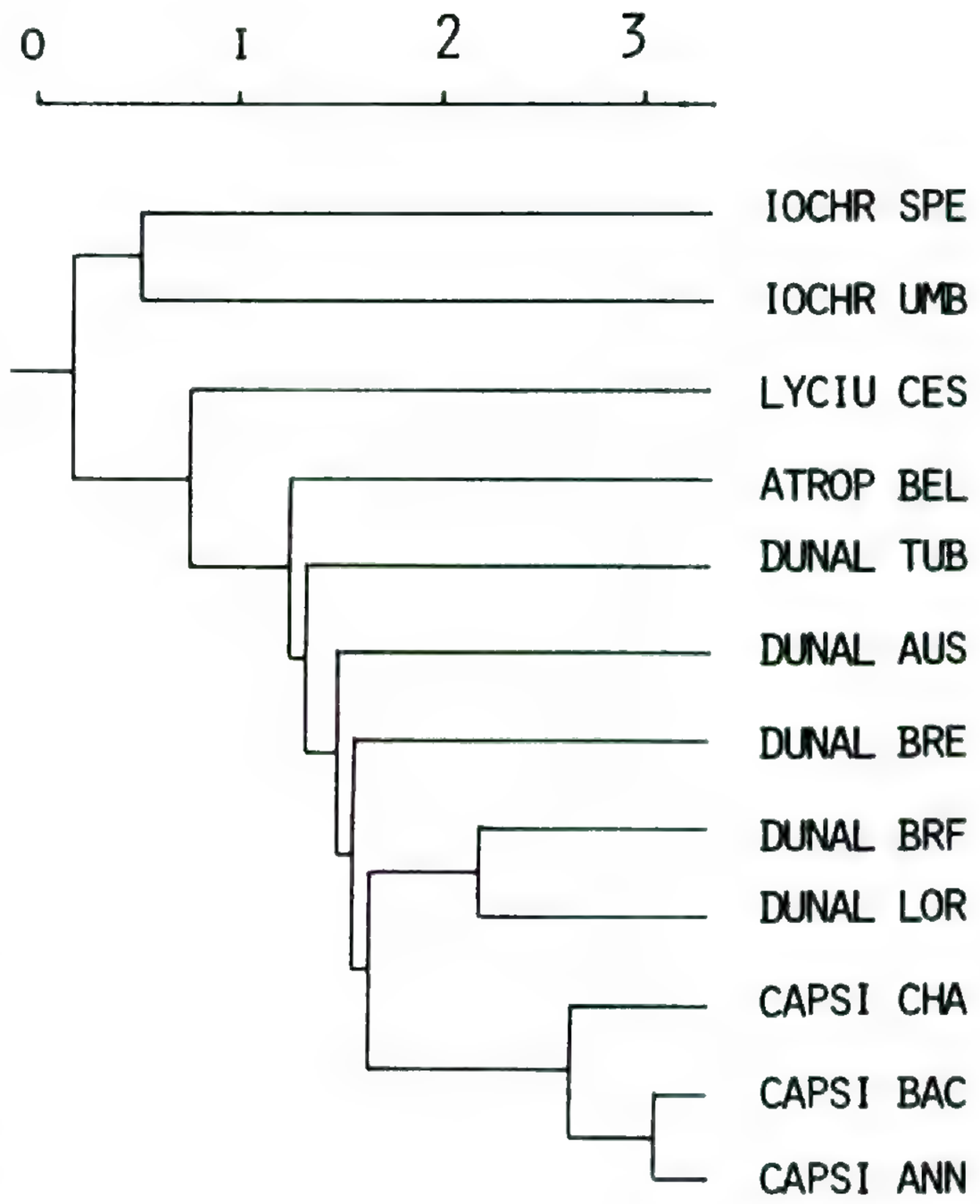

FIGURE 6. Phenogram of immunological similarities of 12 accessions of *Capsicum, Dunalia,* and other genera calculated by dot product and furthest neighbour clustering (for explanation see text and Table 3).

Cladistic analysis using the Dollo method on Felsenstein's Phylogeny Inference Package (PHYLIP version 2.3) (Felsenstein, 1982) produced a rooted tree suggesting an evolutionary sequence with separate branches to *S. aethiopicum, S. hendersonii, S. mauritianum, S. citrullifolium, S. tuberosum, S. simile,* and *S. seaforthianum* (Fig. 3).

It is interesting that the three representatives of subg. *Leptostemonum,* a group with long thin anthers, stellate hairs, and often with prickles, appear to be more ancestral, whereas four representatives of subg. *Solanum* and *Archaesolanum* have a more derived status. This suggestion that subg. *Leptostemonum* is ancestral and that subg. *Solanum* is derived is controversial.

Cladistic analysis by the Wagner method (Felsenstein, 1982) produced an unrooted tree with the species in the same sequence as the Dollo method, but this sequence could be read in either direction.

CAPSICUM AND OTHER GENERA

These were preliminary experiments using antiserum to only *Capsicum annuum.*

A study of 19 genera, mostly of the tribe Solaneae, (Fig. 4) showed the distinctiveness of *Nicandra* from the other genera, which is widely accepted. Some of the serological relationships, such as *Atropa* and *Withania, Physalis* and *Solanum,* and all these with *Lycopersicon,* and possibly also the group of *Datura, Lycium,* and *Witheringia,* agree with taxonomic dispositions based on morphological data, but others, such as the position of *Nicotiana,* disagree.

The relationship of *Dunalia* species to *Capsicum* was surprisingly strong and was therefore investigated by a further study including more species of these two genera and also *Iochroma,* which is sometimes merged with *Dunalia.* The numeric data were analyzed by Similarity Ratio and Group Average clustering (Fig. 5) and by Dot Product and Furthest Neighbour (Fig. 6). In both cases *Capsicum annuum* was grouped with *C. baccatum* and then with *C. chacoense,* the several species of *Dunalia* were grouped fairly close to each other and also to *Capsicum,* and the two species of *Iochroma* were separated from the other taxa. *Lycium cestroides* showed a low level of similarity to anything else: the position of *Atropa belladonna* was different in these two analyses.

The greater similarity of the two cultivated species of *Capsicum* (*C. annuum* and *C. baccatum*) than to the wild one (*C. chacoense*) may be significant. The relationship of *Dunalia* to *Capsicum* indicated here is interesting, because

although the cultivated peppers are mostly annual herbs, the wild relatives are shrubs. Now that these results have suggested it, the similarity of some species of *Acnistus/Dunalia/Vassobia* to *Capsicum* becomes apparent. These relationships deserve further investigation by sexual or somatic hybridization experiments. The separation of *Iochroma* from *Dunalia* in current taxonomic treatments is supported by these data.

Conclusions

The results presented here illustrate the value of immuno-absorption techniques in serotaxonomy, particularly for comparisons of species and genera that are too distinct to allow biosystematic investigations by hybridization experiments.

The relationships indicated within and between the genera *Capsicum* and *Dunalia* are potentially important for taxonomy and plant breeding, but furthermore they are comparable to relationships of different sections within *Solanum*. This emphasizes that the gigantic genus *Solanum*, which is unified by a few floral characters such as poricidal anthers, comprises an assemblage of very diverse taxa, which could be considered as distinct genera.

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NOTES ON THE SYSTEMATICS OF *HESPERANTHA* (IRIDACEAE) IN TROPICAL AFRICA[1]

PETER GOLDBLATT[2]

ABSTRACT

Three species of *Hesperantha* are here recognized in tropical Africa: *H. petitiana* is widespread in highland areas from Ethiopia to eastern Zimbabwe; *H. ballii* is a local endemic of the Chimanimani Mountains in eastern Zimbabwe; and *H. longicollis* occurs in highlands in Malawi and Zimbabwe, extending into eastern Botswana and the Transvaal, South Africa. *Hesperantha petitiana* is taxonomically complex and includes lowgrowing and small-flowered plants corresponding to *Ixia petitiana* and *I. hochstetteriana,* and tall and large-flowered forms corresponding to *H. volkensii* from Mt. Kilimanjaro, and *H. alpina* from Mt. Cameroun. *Hesperantha petitiana* is closely allied to the southern African *H. baurii* complex and is not readily separable from some southern African collections assigned to this alliance. Chromosome numbers are reported for three populations of *H. petitiana,* all polyploid and either tetraploid or hexaploid, in contrast to all southern African plants so far counted, which are diploids.

The genus *Hesperantha* comprises some 55 species of Iridaceae–Ixioideae, all small perennial corm-bearing geophytes. While it occurs widely in Africa (Fig. 1), species are concentrated in southern Africa. There are some 36 species in the winter rainfall region of the Cape Province (Goldblatt, 1984) and about 20 species in the well-watered areas of coastal and montane eastern southern Africa (Goldblatt, 1982; Hilliard & Burtt, 1979, 1982). Six species of *Hesperantha* have been recorded in tropical Africa, from Zimbabwe in the south to Ethiopia in the north, but only three are recognized here. These are the closely allied *H. ballii* Wild and *H. longicollis* Baker (section *Radiata*), and the unrelated *H. petitiana* (A. Richard) Baker (section *Concentrica*), which is variable and often treated as comprising two or more species or varieties. *Hesperantha ballii* and *H. petitiana* are found only in tropical Africa, *H. ballii* being a local endemic of the Chimanimani Mountains of eastern Zimbabwe, while *H. petitiana* occurs in highland areas above 8,000 ft., almost throughout eastern tropical Africa as well as in Cameroun. *Hesperantha longicollis* is centered in the highveld of the Transvaal and Zimbabwe (Obermeyer, 1980) but it extends into Botswana to the west and Malawi to the north.

Both *Hesperantha longicollis* and *H. ballii* are well-defined species, but *H. petitiana* is variable over its wide range and appears taxonomically complex. Moreover, it does not seem particularly distinctive and is difficult to separate from a complex of southern African species centered around *H. baurii* Baker. The variation pattern and taxonomy of *H. petitiana* is dealt with in detail in this paper, while *H. ballii* and *H. longicollis* are discussed only briefly.

Chromosome number has been determined here for three populations of *Hesperantha petitiana,* the species previously unknown cytologically. A collection from Mt. Kilimanjaro (*Puff s.n.*) is tetraploid, $2n$ ($4x$) = ca. 50. Two more populations are hexaploid, one from Ethiopia (*Puff et al. 820911-1/1*) $2n$ ($6x$) = ca. 72 and the other from Mt. Cameroun (*Thomas sub Goldblatt 7272*), $2n$ ($6x$) = ca. 76. Basic chromosome number in *Hesperantha* is $x = 13$ (Goldblatt, 1984) and all of the many other species so far counted, all from southern Africa, have numbers at the diploid level. The counts for *H. petitiana* are interesting because they are the first reports of polyploidy in the genus and also because the numbers recorded suggest a possible $x = 12$ rather than 13 as basic for this species. Unfortunately, the high numbers and small chromo-

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somes make it difficult to establish an exact count and so a second base number in *Hesperantha* remains uncertain.

Hesperantha longicollis

Hesperantha longicollis, typical in *Hesperantha* in being evening blooming, is closely related to the widespread southern African *H. radiata,* which extends from Namaqualand on the west coast, through the southern and eastern Cape to Swaziland in the eastern escarpment. The two have, in common, a curved perianth tube and unusual floral bracts, the outer of which have margins partly united around the axis. The two species can readily be identified by a series of distinguishing features. In *H. longicollis* the flower has a longer perianth tube, 18–25(–30) mm long, well exserted from the bracts; the outer bract is united around the axis only near the base; the leaves are relatively long, usually about half as long as the stem or longer, and plane; and the corm tunics are typically spiny below. In *H. radiata,* the perianth tube is 10–18 mm long, and only slightly exceeds the bracts; the outer bract has margins united around the axis for half to two-thirds its length; the leaves are typically short, about one-third to half as long as the stem, and tend to be thicker in the midrib area; and, at least in populations from eastern southern Africa, the corm tunics are not spiny below (Goldblatt, 1984) although some southwestern Cape forms do have a corm with a spiny base.

Hesperantha longicollis grows in moist habitats, either in vleis, along streams or in seeps, and it blooms at the end of the dry season, typically in August or September. It is most common in the southern African highveld (Fig. 1) and has been recorded from the Transvaal, Northern Cape, extreme eastern Botswana, central and western Zimbabwe, and recently from Malawi, where it was collected by R. K. Brummitt on the Nyika Plateau (*Brummitt 10829*) flowering in May. This represents a significant range extension into tropical Africa of what has been regarded as essentially a southern species.

The species was recently reviewed for "Flowering Plants of Africa" (Obermeyer, 1980), in which a full description and synonymy were provided. This need not be repeated here; however, it should be noted that of the three synonyms cited, *Hesperantha matopensis, H. widmeri,* and *H. sabiensis,* the last does not apply to *H. longicollis.* It is a later synonym of *H. bulbifera* (Goldblatt, 1984), a rare species, unrelated to *H. longicollis,* found on damp cliffs and waterfalls in the Eastern Cape and Transvaal (Goldblatt, 1984).

Hesperantha ballii

Hesperantha ballii is a rare local endemic of the Chimanimani Mountains of eastern Zimbabwe (Fig. 1). It is a small plant, only some 12–25 cm high, with spikes of one to two flowers and narrow, filiform leaves. It is clearly related to *H. longicollis* and *H. radiata,* with which it shares the distinctive floral bracts characteristic of section *Radiata,* united to some extent around the spike axis, and curved perianth tube. In *H. ballii,* the perianth tube is 11–15 mm long, reaching a little beyond the apex of the bracts; the leaves are about 1 mm wide; the outer bracts are united for about 3 mm, about one-fourth their length; and the nearly globose corms apparently have tunics without spines below. The species seems most closely related to *H. radiata,* judging by the similarity of their corms, the length of the perianth tube, and the well-developed union of the outer bracts. It can readily be distinguished from *H. longicollis* by its small size, 1–2-flowered spike, and flowers with a perianth tube only a little longer than the bracts. It is separated from *H. radiata* also by the few-flowered spike, filiform leaves, and the outer bracts being united for ca. 3 mm, only about one-fourth their length, while those of *H. radiata* are united for half to two-thirds their length.

Hesperantha petitiana

As outlined in the introduction, *Hesperantha petitiana* is widespread in highland areas throughout eastern tropical Africa, from Zimbabwe to Ethiopia, with outlying populations to the west in Cameroun (Fig. 1). It is allied to a complex of southern African species centered around *H. baurii,* and it can be distinguished only with difficulty, if at all, from some collections from South Africa and Lesotho. The distinguishing features of *H. petitiana* appear to be its erect, comparatively thick and straight, unbranched stem, straight, 1–3(rarely to 8)-flowered spike, and actinomorphic, straight-tubed pink or white flowers. Like the other pink to reddish or purple-flowered species of the *H. baurii* complex, the flowers open during the day and close at night. Whether the white-flowered forms of *H. petitiana* are also day-blooming is not

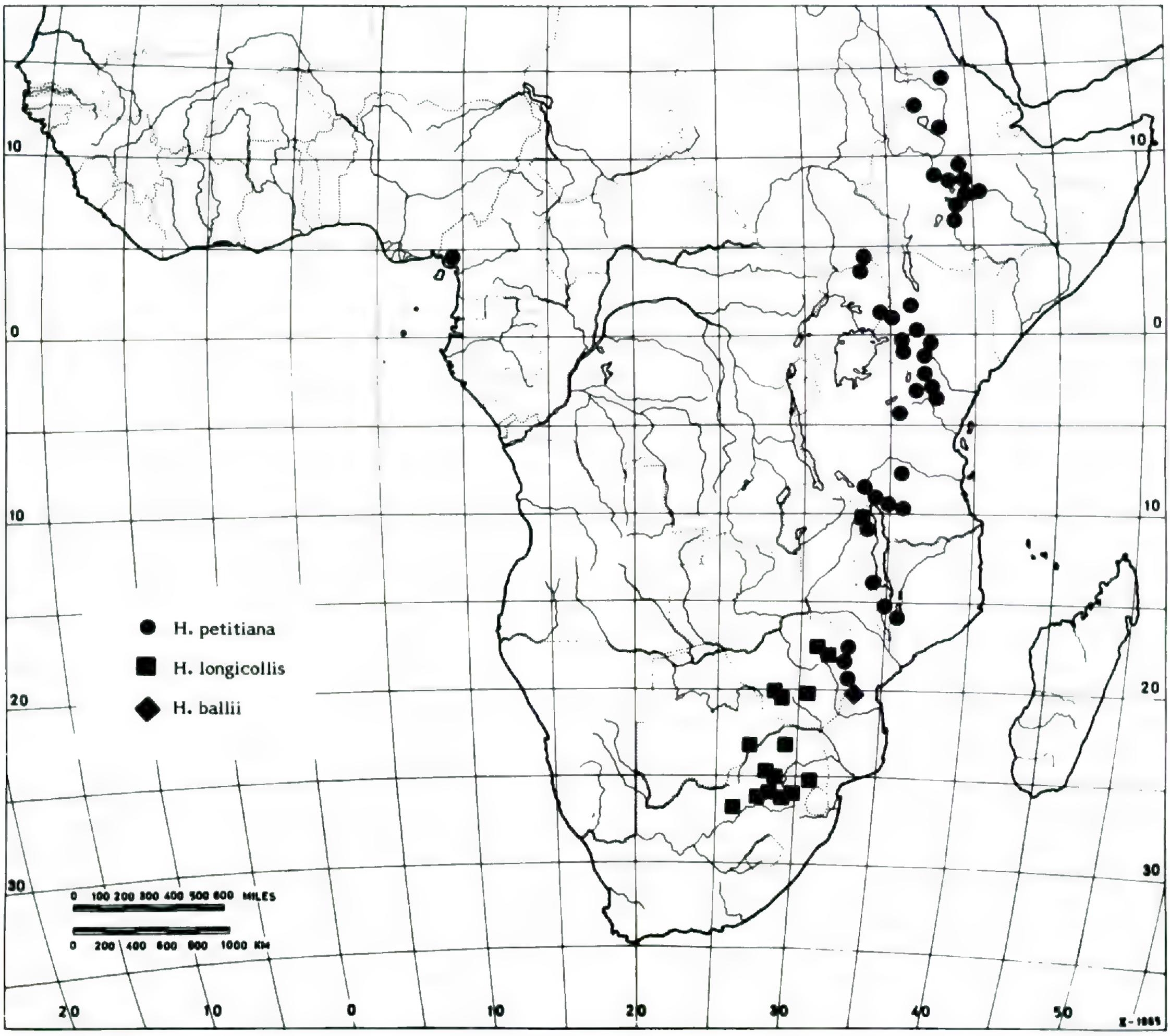

FIGURE 1. Distribution of the tropical African species of *Hesperantha*.

known. Species or races of *Hesperantha* with white flowers are often evening-blooming and those with colored flowers are day-blooming (Goldblatt, 1984) but white-flowered plants in eastern south Africa are generally day-blooming (Burtt, pers. comm.).

The variation pattern in *Hesperantha petitiana* has prompted several authors to admit more than one species or variety in tropical Africa. Originally two species, based on collections of either tall or short plants, were recognized in Ethiopia (Richard, 1850): *Ixia petitiana* and *I. hochstetteriana*. Baker (1898) reduced the dwarf *I. hochstetteriana* to varietal rank as *Hesperantha petitiana* var. *uniflora* Hochst. ex Baker, a treatment followed by Cufodontis (1972) in his "Enumeratio Plantarum Aethiopiae Spermatophyta."

Collections from Cameroun and Tanzania were subsequently described as separate species, *Hesperantha alpina* (as *Geissorhiza alpina*) from Mt. Cameroun by J. D. Hooker in 1864, and *H. volkensii* from Mt. Kilimanjaro by Harms in 1894. *Hesperantha kilimanjarica*, described by Rendle in 1895, is clearly identical to *H. volkensii*. Baker (1898) recognized both *H. alpina* and *H. volkensii* in his treatment of the genus in "Flora of Tropical Africa." Later, Foster (1948) reduced *H. volkensii* to varietal status in *H. petitiana*, commenting that he had some misgivings about even recognizing the variety. Here, I suggest that *H. petitiana* be treated as a single variable species including both *H. alpina* and *H. volkensii*. An analysis of the variation pattern of *H. petitiana* is presented below, in which the Ethiopian populations are discussed first.

ETHIOPIAN COLLECTIONS

Hesperantha petitiana was first discovered in Ethiopia, where it was collected by Schimper and

by Quartin-Dillon and Petit in the mid-nineteenth century. In 1850, Achille Richard described two species of *Hesperantha* (as *Ixia*) from their collections, *I. hochstetteriana* based on Schimper's *I. uniflora* ined., a dwarf form with solitary flowers, and *I. petitiana,* based on taller, 2–3-flowered plants collected by Quartin-Dillon and Petit. The collection that must apparently be chosen as the lectotype of *Ixia petitiana* is in the Paris Herbarium. It comprises several tall plants, about 30 cm high, with 2–3-flowered spikes and four plane, soft-textured leaves, the uppermost almost or entirely sheathing. The flowers have a tube ca. 9 mm long and tepals about 10 mm long and are subtended by herbaceous bracts 10–15 mm long.

Most of the collections made by Schimper comprise dwarf plants under 10 cm long, usually with only three leaves, flowers with tepals ca. 10 mm long, and a tube 6–8 mm long. The type of *I. hochstetteriana, Schimper 185* from Mt. Bachit, Semien 'Bouahit, provinciae Semiene' (also labelled '*Hesperantha uniflora* Hochst. 1239') consists of such plants. However, a collection from 'Berg Gunna,' *Schimper 1182* (B), comprises a range of plants from 7.5 to 18 cm high and with three or four leaves. The taller individuals of the collection are interchangeable with plants from the type collection of *H. petitiana,* while the smaller cannot be distinguished from *I. hochstetteriana.* Another Schimper collection, *579* from 'Acallo Meda' (P), also consists of plants of variable size.

It seems likely on the basis of the available information and collections that the tall *Hesperantha petitiana* and the dwarf var. *uniflora* comprise a single taxon, representing size extremes in a phenotypically plastic species. It is possible that collections of plants of variable size represent a mixture of two species but in the absence of supportive evidence this is unlikely. The apparently continuous variation in some populations and the absence of any consistent morphological distinctions leaves little reason for the recognition of var. *uniflora.* It seems likely that the collections represent the range possible in a high altitude species that grows in situations where plants are subject to a variety of soil and climatic conditions that influence their growth into taller plants often with large flowers or shorter plants usually with smaller flowers.

Among recent collections of *Hesperantha* from Ethiopia there are both dwarf and taller specimens, but no gathering consists entirely of very small plants, as do some of the Schimper collections. Several collections, such as *de Wilde 8109* and *Westphal & Westphal-Stevels 1652,* consist of both small-flowered plants that match *Ixia hochstetteriana* closely, and taller individuals that have larger flowers with tepals 12–15 mm long.

Occasionally collections from Ethiopia are particularly robust (*de Wilde 6574* consists of plants with up to eight flowers on a spike) or have flowers that seem beyond the normal range expected for *H. petitiana* (e.g., *de Wilde 6574*; *Hedberg 4245*) with tepals 15–16 mm long, and bracts 12(–15) mm long. Such collections correspond well with most specimens of *Hesperantha* collected in East Africa that have been described as the separate species, *H. volkensii* Harms.

The significant questions concerning the taxonomy of *Hesperantha* in tropical Africa are the following. Are smaller Ethiopian specimens matching *H. petitiana* different in any taxonomically significant way from the taller and very large-flowered plants form Ethiopia, East Africa (*H. petitiana* var. *volkensii* of several authors), and the Cameroun highlands (*H. alpina*)? A second problem concerns the relationship of the tropical African plants to any southern African species, of which there are several that are obviously closely allied.

EAST AFRICAN COLLECTIONS

Most specimens from East Africa are relatively uniform in flower size, but variable in height and leaf width and thickness. Plants matching the types of *Hesperantha volkensii* and *H. kilimanjarica,* both from Mt. Kilimanjaro, vary in height but reach a maximum of 45 cm, have four leaves, the lower two basal, the third partly sheathing and inserted near the base, all narrow, 2–3 mm wide and with clearly raised margins and midrib, while the fourth is entirely sheathing and inserted in the upper part of the stem. The bracts are (10–)12–15 mm long, and like the larger Ethiopian plants, the flowers are either white or pinkish purple, with a tube 9–10 mm long, tepals 15 mm long, and anthers 5–6.5 mm long.

Plants essentially matching the Kilimanjaro specimens have been collected in highland Uganda, southern Sudan, and Kenya, on Mt. Elgon; the Aberdares, especially Mt. Kinangop; Mt. Kenya and elsewhere. Specimens are sometimes very dwarfed (only 4–10 cm high in *Gillett 18473, Bickford 34*) and with leaves as little as 1 mm

wide, but still with raised margins and midribs, although in several collections a whole range of plant and flower sizes is present (e.g., *Hedberg 1953*; *Gillett 16912*) and it seems that the taller plant matching the types of *H. volkensii* and *H. kilimanjarica,* as well as the smaller ones, all belong to the same species. Occasionally, as in *Battiscombe K715* (Kinohop Plateau), *Napier 719* (Kinangop), *Archer 676* (Namanga Hill), and a few others, the leaves are broader, and the margins and midrib less obviously raised, as in most Ethiopian specimens, but these are also connected by a series of intermediates to the typical Kilimanjaro form.

In Tanzania, the tall, Kilimanjaro form appears common at higher elevations throughout the Kilimanjaro Range and in the Southern Highlands, is sometimes robust and with leaves 3–4 mm wide, but also sometimes small. A collection made by Schlieben (*4918*) on Kilimanjaro is of especial interest. Plants range in size from 8–20 cm high and the tallest plants apparently match *H. volkensii* in every respect. The shorter individuals have smaller flowers, and in specimens at the Zurich and Stockholm herbaria the tepals may be as short as 10 mm. These plants can barely, if at all, be distinguished form the type material of the dwarf *Ixia hochstetteriana* from Ethiopia.

In the Southern Highlands plants tend to have more soft-textured leaves, 3–5 mm wide, and often have spikes with 6 or more flowers, but the fewer-flowered individuals appear to match in all respects plants from Kilimanjaro. In Malawi, the southern Tanzania form has been collected in all the higher areas including the Nyika Plateau, the Dezda Mountains, and Mt. Mlange. Further south in Zimbabwe, apparently the same form has been collected along the eastern highlands from Inyanga to the Vumba Mountains, where it is currently identified either as *H. petitiana* or as the southern African *H. baurii,* a name in current use for a complex probably including several species but not yet understood. In southern Africa there are several collections that appear to match exactly the Malawi and south Tanzania form of *H. petitiana,* but the entire *H. baurii* complex awaits further study before the systematics of the genus in this area can be resolved. However, I suggest that, for the present, all collections of *Hesperantha* occurring from Zimbabwe north to Kenya be assigned to the single taxon, *H. petitiana.*

Hesperantha alpina from Cameroun is poorly known and only a few gatherings have been made. Specimens in the Berlin collection comprise dwarf, 3- or 4-leaved individuals in fruit (*Mann 2134*) and very tall plants with buds or closed flowers (*Preuss 968*). The dwarf plants match *Ixia hochstetteriana* well, while the tall plants are a fair match for *H. volkensii* but appear to have rather small flowers, perhaps not fully developed. The morphology and the range of size in these specimens corresponds closely with the more ample Ethiopian and Kenyan collections and I cannot distinguish the Cameroun plants other than by their origin. *Hesperantha alpina* is accordingly reduced here to synonymy in *H. petitiana.*

The treatment of the variable *H. petitiana* complex as a single species throughout tropical Africa seems the only consistent way in which to deal with the degree of variability encountered in the complex. None of the variation is strictly geographical, and both tall, large-flowered plants and dwarf, smaller flowered plants may be found almost throughout its range, though the latter appear more frequent in Ethiopia.

The taxonomy and nomenclature of *Hesperantha petitiana* is confusing and the extensive synonymy and a description are presented below:

Hesperantha petitiana (A. Richard) Baker, J. Linn. Soc., Bot. 16: 96. 1878 et Fl. Trop. Africa 7: 348–349. 1898; Cufodontis, Enum. Pl. Aethiopiae Sperm. 2: 1588. 1972. *Ixia petitiana* A. Richard, Tent. Fl. Abyss. 2: 309–310. 1850. TYPE: Ethiopia, near 'Maygouagoua,' Sept., '*Ixia petitiana* Nob.' *Quartin-Dillon & Petit s.n.* (lectotype, P, here designated).

Ixia hochstetteriana A. Richard, Tent. Fl. Abyss. 2: 309. 1850. TYPE: Ethiopia, Mt. Bachit: Semien (Mt. Bouahit, Prov. Semiene), Aug., '*Hesperantha uniflora* Hochst.' *Schimper 1239* (lectotype, P, here designated; isolectotypes, B, BM, BR, G, L, S, Z). *Geissorhiza abyssinica* var. *parvula* Klatt, Linnaea 34: 717. 1866. *Hesperantha petitiana* var. *uniflora* Hochst. ex. Baker, Fl. Trop. Africa 7: 349. 1898; Cufodontis, Enum. Pl. Aethiopiae Sperm. 2: 1588. 1972.

Hesperantha uniflora Hochst. ms (*Schimper 185* etc.); Richard, Tent. Fl. Abyss. 2: 309. 1850, in synon.

Geissorhiza alpina Hook. f., J. Linn. Soc., Bot. 7: 223. 1864. *Hesperantha alpina* (Hook. f.) Pax ex Engler, Hochgebirgefl. Afrika 174. 1892. Abh. Preuss. Akad. Wiss., Phys.-Math. Kl. 1891: 1–461. 1892 [Mar.]; Hepper, Fl. W. Trop. Africa 3: 141. 1968. TYPE: Cameroun. Cameroun Mt., 9,000–10,000 ft., Nov. 1862, *Mann 2134* (lectotype, K; isolectotype, B).

Hesperantha volkensii Harms, Bot. Jahrb. Syst. 19 (Beibl. 47): 28. 1894. *Hesperantha petitiana* var. *volkensii* (Harms) Foster, Contr. Gray Herb. 166: 22. 1948; Hedberg, Symb. Bot. Uppsal. 15: 68–69. 1957. TYPE: Tanzania, 'Kilimandscharo': 2,440 m, *Volkens 783* (lectotype, B; isolectotypes, BM, G).

Hesperantha kilimanjarica Rendle, J. Linn. Soc., Bot. 30: 402. 1895. TYPE: Tanzania. Mt. Kilimanjaro: above Morong, to 10,000 ft., 1888, *Taylor s.n.* (holotype, BM).

Geissorhiza abyssinica R. Br. ex A. Richard sensu Klatt, Linnaea 34: 716. 1866, non *G. abyssinica* R. Br. ex A. Richard (Tent. Fl. Abyss. 2: 308. 1850). [= *Lapeirousia abyssinica* (R. Br. ex A. Richard) Baker, the types being: Ethiopia. Near 'Maygouagoua': Sept., *Quartin-Dillon & Petit s.n.*; Selleuda prope Adowa, *Schimper s.n.*].

Plants (8–)12–30(–45) cm high. *Corm* 7–12 mm diam. with dark brown, concentric, usually woody tunics. *Cataphyll* membranous. *Leaves* (3–)4, the lower two basal, the third usually inserted near the base or in the lower part of the stem and sheathing in the lower half, the fourth leaf, if present, inserted in the mid to upper part of the stem and often entirely sheathing, 2–6 mm wide, usually about half as long as the stems, margins and midrib barely to moderately thickened. *Stem* erect, smooth, unbranched. *Spike* (1–)2–6(–9)-flowered, straight to slightly flexuose; *bracts* herbaceous, becoming membranous toward the apex, (9–)12–15 mm long, the inner narrower and slightly shorter. *Flowers* actinomorphic, stellate, white to pink, outer tepals flushed dull red to brown on reverse; *perianth tube* cylindric, 6–9 mm long; *tepals* subequal, (9–)12–18 mm long, narrowly ovate to elliptic, 5–7 mm at widest point. *Filaments* 3–4 mm long; *anthers* (3–)4–7.5 mm long. Ovary 2–3 mm long, style branches 6 mm long. *Capsule* obovoid, 7–10 mm long, somewhat shorter to slightly exceeding the bracts. *Chromosome number* $2n$ = ca. 50, ca. 72–76.

Flowering time. July–December in Ethiopia; May–August and December–February in Kenya, Uganda, and northern Tanzania; March–May in S. Tanzania, Malawi, and Zimbabwe; September in Cameroun.

Distribution. Highlands in Ethiopia, southern Sudan, eastern Uganda, Kenya, Tanzania, Malawi, Cameroun, and eastern Zimbabwe. Figure 1.

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CYTOLOGY AND SYSTEMATICS OF THE *MORAEA FUGAX* COMPLEX (IRIDACEAE)[1]

PETER GOLDBLATT[2]

ABSTRACT

The *Moraea fugax* complex, widespread in the winter rainfall area of southern Africa, is treated here as comprising three species, *M. gracilenta* and the new *M. macrocarpa,* both of restricted distribution and morphologically and cytologically uniform, and the very widespread and variable *M. fugax*. The latter comprises two subspecies: larger flowered populations of robust plants with large capsules and one or two channeled leaves are referred to subsp. *fugax* while small-flowered forms with small capsules and usually two filiform leaves are referred to subsp. *filicaulis*. Cytologically *M. fugax* is remarkably variable. Basic chromosome number in *Moraea* and in the complex is $x = 10$, and $n = 10$ is the only number known for *M. gracilenta* and *M. macrocarpa*. *Moraea fugax* subsp. *fugax* has a base number of $x = 10$ but exhibits an extensive aneuploid series with populations or races having $n = 9$, 8, 7, 6, and 5. Subspecies *filicaulis* has haploid numbers of $n = 9$, 6, and 5, the former perhaps basic for this taxon. Some correlation of morphological and karyotypic variation suggests that aneuploid decrease occurred in several morphological lines as geographical races differentiated from the ancestral stock during alternating dry and wet phases of the Quarternary. A revised classification of the complex is presented in the second half of the paper, following a detailed description of the karyological and morphological variation. The karyology of *M. fugax* is not completely known, but the major features are probably reflected in the data presented here.

The *Moraea fugax* complex (*Moraea* sect. *Subracemosae* sensu Goldblatt, 1976a) is one of the most taxonomically complex groups in this pan African genus of some 120 species. *Moraea fugax* is the major taxon of the section with one or more distinctive segregates sometimes recognized as varieties or separate species. The section has been variously treated in the past as comprising one species and four varieties as in "Flora Capensis" (Baker, 1896) or as three species (Baker had added two new species to the complex by 1906). In the most recent revision of *Moraea* in the winter rainfall area of southern Africa, only two species (Goldblatt, 1976b) were recognized, the uniform and local *M. gracilenta* Goldbl. and the widespread and variable *M. fugax* (de la Roche) Jacq. [(= *M. edulis* (L. f.) Ker]. The complex is distinctive in its vegetative habit. The branches are short and often clustered in a semi-umbellate manner, and the one or two foliage leaves are inserted near the stem apex at the point of branching, usually well above the ground. The flowers are of the basic type for the genus with large outer tepals marked with nectar guides, smaller inner tepals, and large flattened style branches with well-developed crests, but the capsules are distinctive in having a well-developed beak. Morphological variation is extensive and confusing. Several races can be distinguished in *M. fugax* but the existence of many intermediates has made recognition of additional species or subspecies difficult and impractical.

Since my revision I have had the opportunity to observe and collect members of the complex extensively in the field. As a result I have a deeper understanding of the patterns of morphological variation and have assembled considerably more cytological data. This new information has made a review of the complex necessary. I now recognize three species in the complex: *M. gracilenta*; the new *M. macrocarpa,* comprising dwarf, blue-flowered and often unbranched plants with long capsules and nearly sessile spathes; and *M. fugax* with two subspecies, *filicaulis* (Baker) Goldbl., including dwarf plants with small, white to cream or rarely blue flowers, small capsules, and stalked spathes, and subsp. *fugax* for larger flowered, robust plants with either white, blue, or yellow flowers and large capsules. Along the west coast several races or forms of subsp. *fugax*

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TABLE 1. Chromosome number and collection information for previously published and original counts presented in this paper for *Moraea* sect. *Subracemosae*. Original counts are in bold print.

Species	Diploid Number ($2n$)	Collection Data
M. gracilenta	20	below Piekenierskloof Pass, *Goldblatt 3279* (MO).
	20	riverside, Clanwilliam campsite, *Goldblatt s.n.*
M. macrocarpa	**20**	mountains W of Trawal, *Goldblatt 5661* (MO); farm Reiers Rus near Worcester, *Goldblatt & Snijman 6961* (MO); near Piketberg, *Anon s.n.* ex hort. Kirstenbosch.
M. fugax subsp. *fugax*	**20**	Olifants River Bridge, near Klawer, *Goldblatt 2828* (MO); mountains W of Trawal, *Goldblatt 5667* (MO); NW of Nieuwoudtville, *Goldblatt 5843* (MO).
	18	near Wallekraal, Namaqualand, *Goldblatt s.n.* no voucher; Bokbaai road, *Goldblatt 5850* (MO); Donkergat Peninsula, *Goldblatt s.n.* no voucher; near Robertson, *Goldblatt 5860* (MO); near Brandewyn River, *Goldblatt 4812* (MO); Cedarberg at Algeria, *Viviers s.n.* (MO); farm Reiers Rus near Worcester, *Goldblatt & Snijman 6962* (MO).
	16	8 km N of Malmesbury, *Goldblatt 3025* (MO).
	16	commonage at Malmesbury, *Goldblatt 4813* (MO); 20 km NW of Malmesbury, *Goldblatt 4081* (MO); sandy soil at Klawer, *Goldblatt 5662* (MO); Pakhuis Pass near Leipoldts Grave, *Goldblatt s.n.* (MO).
	14	Cape Point Reserve, *Goldblatt 5403* (MO); Caledon Zwartberg, Swartrivier, *Goldblatt 5782* (MO); near Velddrif, sandy plains, *Goldblatt s.n.* (MO).
	12	Hopefield, *Goldblatt 152* (J).
	12	foot of the Elandskloof Mts., Elandsberg farm, *Goldblatt 5851* (MO); near Bellville, *Delpierre s.n.* no voucher; Silvermine, Cape Peninsula, *Goldblatt 5164* (MO).
	10	*(cytotype A, southwestern Cape populations):* Malmesbury, near Abbotsdale, *Goldblatt 5116* (MO); foot of Houw Hoek Pass, *Goldblatt 4292* (MO); slopes of Koeberg, N of Cape Town, *Goldblatt 4080* (MO); Kommetje, Cape Peninsula, *Goldblatt s.n.* no voucher; Paarl flats, *Goldblatt s.n.* no voucher; Cape Peninsula, foot of Klaasjagersberg, *Goldblatt 5264* (MO).
		(cytotype B, Olifants River Valley populations): foot of the Winterhoekberg N of Klawer, *Goldblatt 5778* (MO); Olifants River Valley, near Clanwilliam, *Goldblatt 5936* (MO).
M. fugax subsp. *filicaulis*	**18**	Ramskop, Clanwilliam, *Goldblatt 7376* (MO).
	12	Gifberg slopes, *Goldblatt 207* (BOL).
	12	granite hills near Kamieskroon, *Goldblatt 4254* (MO); Kamiesberg, Rooiberg slopes, *Goldblatt 4308* (MO); Richtersveld, Eksteenfontein road, *Goldblatt 5717* (MO).
	10	flats below Wildeperdehoek Pass, *Goldblatt 5761* (MO); hills W of Trawal, Kleipan road, *Goldblatt 5666* (MO).

can be recognized, each distinguished by small differences in morphology such as flower color, vegetative size, leaf number, and occasionally in the relative proportions of floral parts. The different races displace one another either geographically in suitable habitats or less often temporally. Where subsp. *fugax* is sometimes sympatric with subsp. *filicaulis* or *M. macrocarpa* it usually flowers at the same time, but no hybrids or intermediates are known.

Until now chromosome information for the complex has been limited (Goldblatt, 1971, 1976a, 1976b). *Moraea gracilenta* was reported to have a diploid number of $2n = 20$, and $x = 10$ is presumably basic for the complex. But $2n = 16$ was recorded in one population of *M. fugax* and $2n = 12$ in two others, one a large white-flowered form and the other corresponding to the dwarf and slender stemmed *M. filicaulis* Baker. Numerous chromosome counts are now available (Table 1). New data indicate that *Moraea gracilenta* and *M. macrocarpa* are cytologically uniform ($2n = 20$), but the more widespread *M. fugax* now appears remarkably variable

chromosomally. Chromosome numbers range from $2n = 20$ to $2n = 10$ in subsp. *fugax* and $2n = 18$, 12, and 10 in subsp. *filicaulis*. Variation in the karyotype is correspondingly extensive, and karyotypes range from predominantly acrocentric complements with $2n = 20$ or 18 and medium to small chromosomes, to those with $2n = 16$, 14, 12, or 10 and one to three large metacentric pairs and much smaller acrocentrics. The total amount of chromosome material seems fairly constant (Table 2) in all karyotypes, based on a comparison of total chromosome length. Polyploidy has played no role in numerical changes in the complex that thus stands out as a group where aneuploidy alone has apparently resulted in the extreme karyotypic variability.

TABLE 2. Mean total length of the chromosome complement in selected populations of *Moraea fugax* and *M. gracilenta*.

Species	Length (cm)	Length (μm)
M. gracilenta		
$2n = 10$ (Clanwilliam)	19.4	87.4
M. fugax subsp. *fugax*		
Large white-flowered form		
$2n = 20$ (Klawer)	23.2	104.5
$2n = 20$ (Trawal)	21.8	90.2
$2n = 18$ (Donkergat)	19.1	86
$2n = 14$ (Velddrif)	20.8	93.6
Late-blooming blue-flowered form		
$2n = 12$ (Silvermine)	23.6	106.2
Large yellow-flowered form		
$2n = 10$ (Houw Hoek)	22.4	100.9
M. fugax subsp. *filicaulis*		
$2n = 12$ (Kamieskroon)	19.8	88.9

RELATIONSHIPS

The complex, as sect. *Subracemosae*, was assigned to subg. *Moraea* (Goldblatt, 1976a) largely because of its generalized flower and basic chromosome number, $x = 10$, which corresponds to the base number for the genus. It is apparently allied to sect. *Deserticola* (five species), which occurs in the drier parts of the Cape west coast and in southern Namibia. The species of sect. *Deserticola* all have a basal or nearly basal leaf and an open branching system but resemble sect. *Subracemosae* in the tendency to develop a short beak on the capsule, especially *M. macgregorii* Goldbl.

GEOGRAPHICAL DISTRIBUTION

The section is restricted to the winter rainfall region of southern Africa and extends along the west coast from just south of the Orange River to Knysna on the south coast (Fig. 1), a distance of some 900 km. *Moraea gracilenta* has a limited range at the foot of the mountains and intermontane valleys from Tulbagh to Clanwilliam in the Olifants River Valley. *Moraea macrocarpa* is equally restricted in its range and occurs in deep, coarse sand mainly on the west coast from Saldanha to Clanwilliam but also in the Breede River Valley near Worcester. *Moraea fugax* is found throughout the range of the section. Records are few and scattered east of the Caledon and Worcester districts but *M. fugax* has been collected at Knysna on the south coast some 400 km east of Cape Town and has even been reported from Humansdorp (Moriarty, 1982), but specimens are needed to confirm this. The complex is clearly infrequent east of Caledon and evidently less variable there. Subspecies *filicaulis* is common in Namaqualand, but it extends south along the west coast into the Olifants River Valley south to Clanwilliam. Its range overlaps that of subsp. *fugax* and the two are sympatric at several localities.

METHODS

CYTOLOGY

All chromosome observations were made at mitotic metaphase in root tip squashes. Root tips from either sprouting corms or germinating seeds were harvested in midmorning and pretreated in 8-hydroxyquinoline at refrigerator temperatures for seven to eight hours, before fixation in ethanol-acetic acid (3 : 1) for two to three minutes. The tips were then either stored in 70% ethanol or immediately hydrolyzed in 10% HCl for six minutes before being transferred to water. Root tip apices were squashed in lacto-propionic orcein (Dyer, 1963) or FLP orcein (Jackson, 1975).

With few exceptions, the plants used in the study were collected in the wild by myself (Table 1), and voucher specimens were made for plants in suitable condition. Unvouchered accessions will be grown, wherever possible, to flowering and then pressed. Vouchers have been placed in the Missouri Botanical Garden Herbarium (MO).

The method used here differs from that employed previously (Goldblatt, 1971, 1976a) in

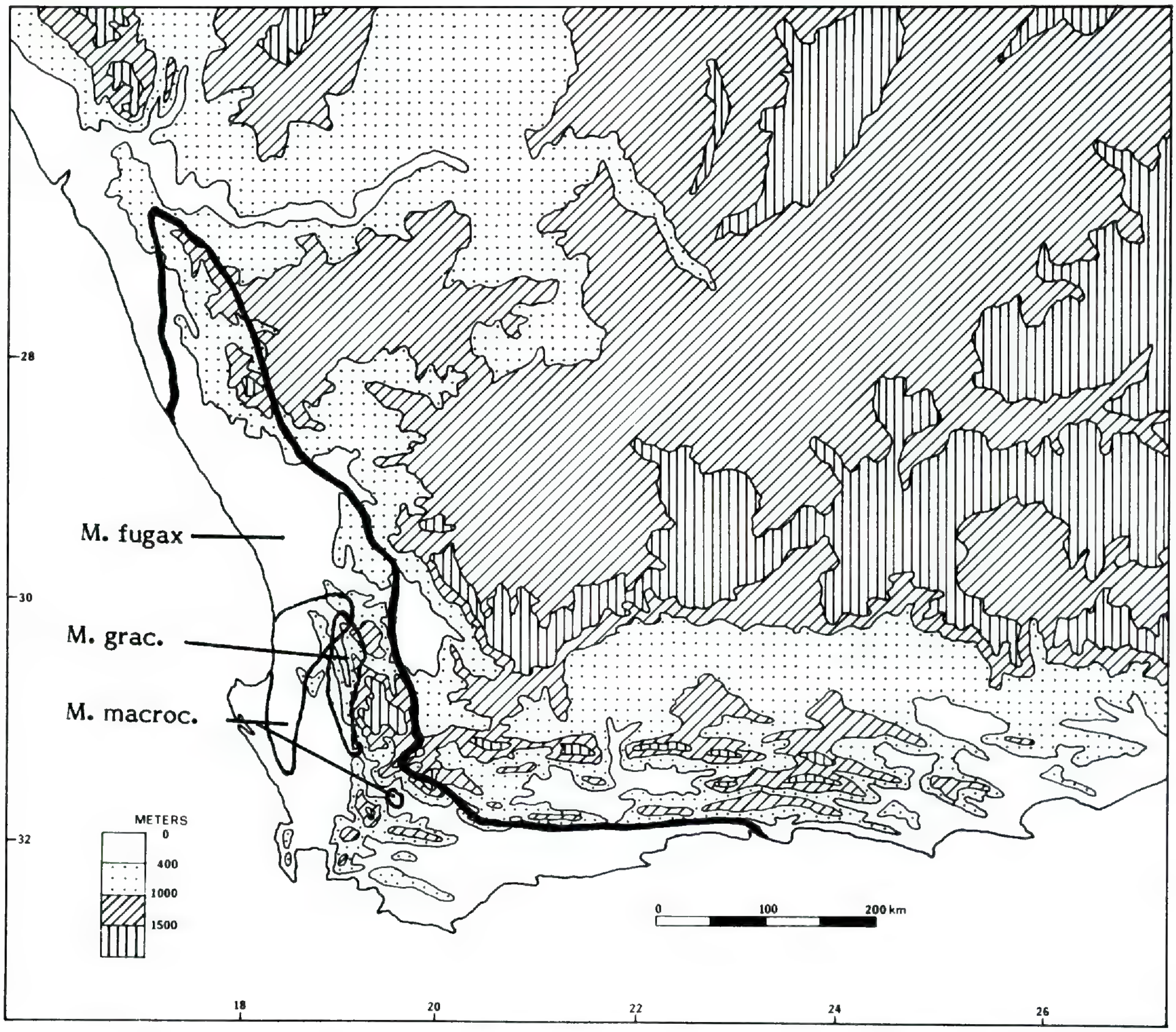


FIGURE 1. Geographical distribution of *Moraea fugax, M. gracilenta,* and *M. macrocarpa.*

my studies of *Moraea* cytology, so that measurements are not directly comparable. All figured metaphases are drawn at the same scale. Metaphases selected for illustration are representative of a particular population or karyotype group (Figs. 2, 4, 5). Minor differences between karyotypes of different populations have not been figured for reasons of economy of space, and while these differences may be significant, they are not of the same magnitude as those dealt with here.

TAXONOMY

Live material of all species and numerous populations was examined before preservation, and illustrations were made from living plants. Specimens from the herbaria with important southern African collections were also studied. Measurements were made from live plants when possible but also include the variation found in dry material, in which the delicate parts of the flowers shrink some 10–15%. Flower color fades progressively in dry specimens, eventually changing completely, sometimes becoming darker and usually disappearing. Color notes on collected specimens are desirable and are frequently mentioned by collectors.

Material examined is cited according to the grid reference system based on geographical degree co-ordinates of latitude and longitude in current use in southern Africa (Edwards & Leistner, 1971).

KARYOTYPES

A chromosome number of $2n = 2x = 20$ occurs in *Moraea macrocarpa, M. fugax* subsp. *fugax,* and *M. gracilenta,* and I believe it is basic for *Moraea* and for the complex. *Moraea fugax* subsp. *fugax* is cytologically heterogeneous and

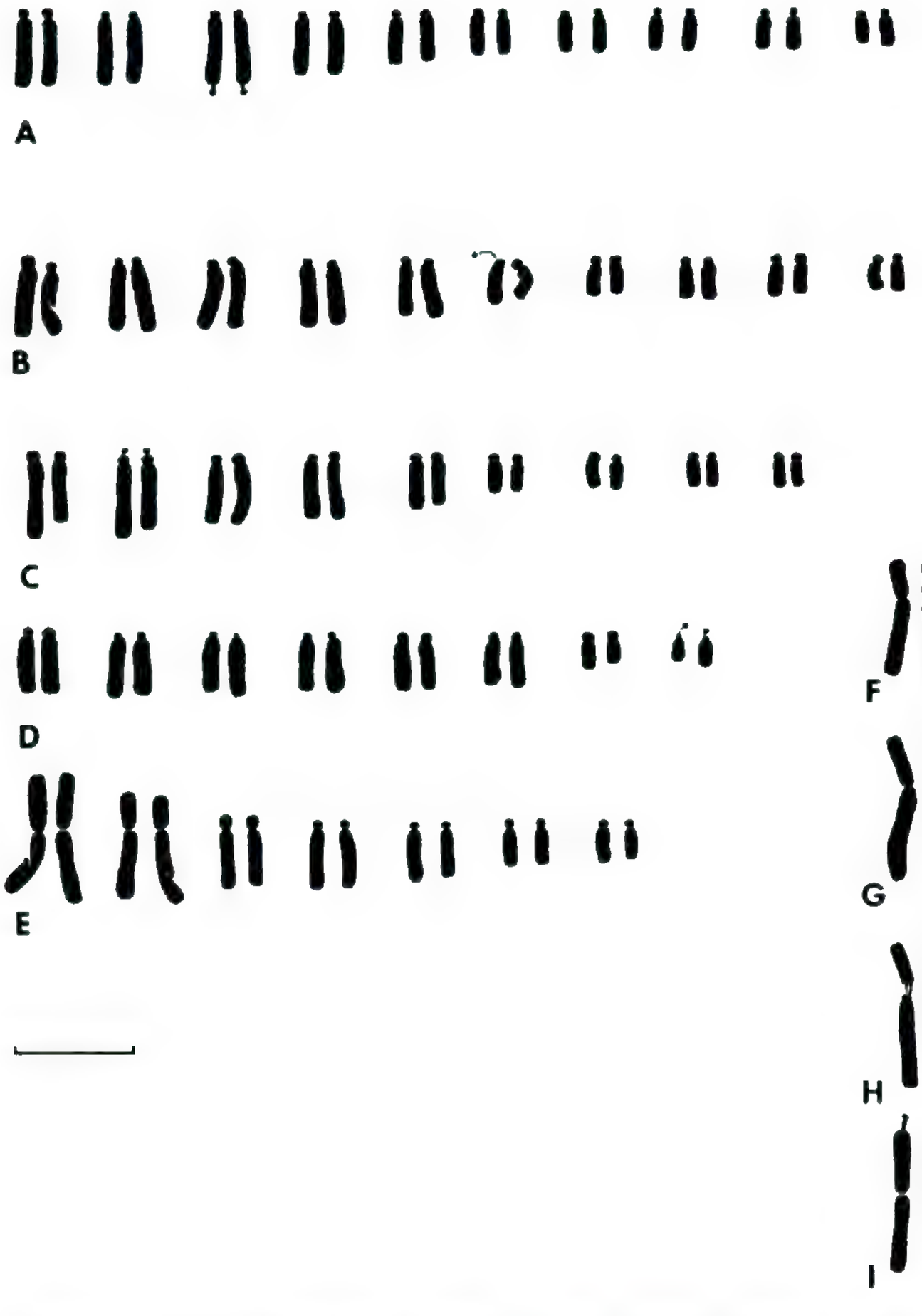


FIGURE 2. Chromosome cytology of the *Moraea fugax* complex.—A. Mitotic chromosomes of *M. macrocarpa*, $n = 10$. B–I. *Moraea fugax* subsp. *fugax*. B–E. Large white-(pink-)flowered form.—B. Kleipan road near Trawal, $n = 10$.—C. Donkergat Peninsula, $n = 9$.—D. Near Klawer, $n = 8$.—E. Velddrif road, $n = 7$. F, G. Blue-purple-flowered form.—F. Cape Point, $n = 7$.—G. Silvermine, Cape Peninsula, $n = 6$. H, I. Small white-flowered form.—H. Malmesbury, $n = 8$.—I. Near Gouda, $n = 6$. Scale = 10 μm.

also has $2n = 18$, 16, 14, 12, and 10 (Figs. 2, 4). *Moraea fugax* subsp. *filicaulis* has $2n = 18$, 12, and 10 (Fig. 5). Karyotypes vary considerably but are usually similar for each diploid number. They are briefly described in the following paragraphs. Voucher data and chromosome number for all populations examined are presented in Table 2.

MORAEA GRACILENTA, M. MACROCARPA & M. FUGAX SUBSP. *FUGAX* $2n = 20$ CYTOTYPE

Eight populations, including two of *Moraea gracilenta*, three of *M. macrocarpa* (Fig. 2A), and three of *M. fugax* (Fig. 2B), have $2n = 20$ and similar karyotypes with strongly acrocentric chromosome pairs. Variation in chromosome length is appreciable, the longest being about twice the shortest. Four to five large chromosome pairs (7–8 μm long), one to two medium pairs, and four (or five) short pairs (3–4 μm long) can be recognized. Satellites, not consistently observed, are on a short pair.

MORAEA FUGAX SUBSP. *FUGAX* $2n = 18$, 16, 14 & 12 CYTOTYPES

1. 2n = 18 karyotypes (tall white- and smaller yellow-flowered forms). The seven populations of *Moraea fugax* subsp. *fugax* with $2n = 18$ have karyotypes similar to those with $2n = 20$. There are five long and four short pairs of acrocentric chromosomes. One individual of a population from Donkergat Peninsula (*Goldblatt s.n.*) is structurally heterozygous with 11 long and seven short chromosomes. Two other individuals of the population had ten long and eight short chromosomes. Satellites were seen clearly only in the

Donkergat population on the short arms of a long chromosome pair (Fig. 2C).

*2. 2*n = *16 karyotypes (white- and pink-flowered forms).* Five populations have $2n = 16$. Three of these are a distinctive white-flowered form with narrow tepals from the Malmesbury area. The karyotype of this form (Goldblatt, 1976a; Fig. 1G) comprises a long acrocentric pair with conspicuously large satellites, four only slightly shorter acrocentric pairs, and three short acrocentric pairs (Fig. 2H). Another population matching this form has $2n = 12$ (Fig. 2I) (see below).

A second karyotype, with $2n = 16$, was found in a single unusual, pale pink-flowered population from the Olifants River Valley (*Goldblatt 5662*) and consists of six medium to long acrocentric and two short acrocentric pairs, one of which has small satellites (Fig. 2D). This karyotype is quite different from the white-flowered Malmesbury form with $2n = 16$ and must be of independent origin.

A yellow-flowered population from Pakhuis Pass also has $n = 16$ (Fig. 4A). The karyotype comprises one long submetacentric pair, and the remainder are strongly acrocentric. One of the longer of these pairs has a small satellite located at the end of a long arm, a feature of most populations of yellow-flowered plants studied.

*3. 2*n = *14 karyotypes (white, yellow, or blue forms).* Three populations, each morphologically distinct, have $2n = 14$. One of these, a large yellow-flowered form from Caledon Zwartberg (*Goldblatt 5782*), has one pair of large metacentrics (16 μm long), five medium-sized pairs (8–10 μm long) two of which are acrocentric, two telocentric, one metacentric, and a tiny acrocentric pair (Fig. 4B). There are satellites on one of the telocentrics. Other plants matching this relatively short-stemmed but large yellow-flowered form have $2n = 10$ and three large metacentric chromosome pairs.

A second population with $2n = 14$ is a blue-flowered and late-blooming form from the Cape Peninsula. The karyotype comprises a long submetacentric pair, ten strongly acrocentric medium-sized pairs, and one very short acrocentric pair (Fig. 2F). Satellites were not readily seen but appeared to be on the long arm of one of the medium-sized acrocentric pairs. Other populations of this form have $2n = 12$, and their karyotypes differ by a very long metacentric pair.

The third population with $2n = 14$ was collected near Velddrif on the west coast and had large white flowers. The karyotype comprises a long metacentric pair, two long and one medium pair, and two short pairs (Fig. 2F). Most populations of this tall white-flowered form have $2n = 20$ or 18, but $2n = 12$ has been recorded from one locality (Goldblatt, 1971).

*4. 2*n = *12 karyotypes (large white- or blue-flowered forms).* Four populations have $2n = 12$. Three of these, all from the southwest Cape, represent the large blue- (to white-) flowered and moderately robust late-blooming form common in sandy soils. The karyotype (Goldblatt, 1971) is similar in all populations. There are two long metacentric pairs, three medium-sized acrocentrics, and a tiny acrocentric pair (Fig. 2G). Satellites were seen occasionally on the longest and shortest pairs. A white-flowered population from near Gouda (*Goldblatt 5851*) has a similar karyotype (Fig. 2I), but the plants are apparently identical with the slender white-flowered form with narrow tepals from the Malmesbury area having $2n = 16$.

*5. 2*n = *10 karyotypes (large yellow-flowered forms).* Of the eight populations with $2n = 10$, six represent the large yellow-flowered, typical form of *Moraea fugax* from the southwestern Cape. The karyotype (Fig. 4C) consists of two metacentric pairs 13–14 μm long, one submetacentric 12–13 μm long, and two much shorter acrocentrics 7–8 μm long. Satellites are on the end of the long arm of a short pair and the longest of the two metacentric pairs.

The second karyotype of subsp. *fugax* with $2n = 10$ occurs in yellow-flowered populations in the Olifants River Valley (Fig. 4D). It comprises two long metacentrics, a medium-sized meta- to submetacentric, a medium-sized acrocentric, and a pair of tiny subtelocentrics with large satellites. A second pair of satellites was seen, in one population (*Goldblatt 5778*), on the longer arm of the longest metacentric pair. These populations are notable in having nearly erect inner tepals, and they differ from the southern yellow-flowered form in this feature as well as in details of their karyotype.

MORAEA FUGAX SUBSP. *FILICAULIS*

Only one population of subsp. *filicaulis* has so far been found, with $2n = 18$, from Clanwilliam in the far south of its range. This karyotype comprises ten long and eight short chromosomes, all strongly acrocentric. Two central Namaqualand populations have $2n = 12$. One of these is a small,

TABLE 3. Comparison of some critical morphological characteristics of the species of *Moraea* sect. *Subracemosae*. Color key: bl = blue; ye = yellow; wh = white.

Species	Branches	Spathes (cm)	Outer Tepal (cm)	Capsule (mm)	Anther (mm)	Color
M. gracilenta	many, open	2.5–3.5	2–2.6(–3)	8–12	4–6.5	bl
M. macrocarpa	few, sessile	4–5(–6.5)	2–3	(18–)20–25	4–5	bl
M. fugax subsp. *filicaulis*	several, usually congested	2–3.5(–4)	2–2.6(–3.1)	9–13(–15)	4–5(–6)	bl, wh
M. fugax subsp. *fugax*	several, usually congested	(3.5–)4–6	2.7–4	15–22	5–10	bl, wh, ye

dark blue-violet-flowered form that corresponds to the type of Baker's *M. filicaulis*. The other population has white flowers. The karyotype consists of two pairs of long acrocentrics and a graded series of smaller acrocentrics (Fig. 5A). There are very large satellites on the short arm of one of the longest pairs.

A population from the southern Richtersveld, in the extreme north of the range of *Moraea fugax*, also has $2n = 12$ but has a different karyotype (Fig. 5B) comprising a long metacentric pair, a fairly long submetacentric (-acrocentric) pair, three medium-sized acrocentric pairs, and an unusual small metacentric pair. Small satellites are on the long arms of a medium-sized chromosome pair. This is somewhat similar to karyotypes in the two populations with $2n = 10$, which have one long metacentric and four medium-sized acrocentric pairs and lack the short metacentric pair (Fig. 5C). The populations with $2n = 10$ are from opposite ends of the range of subsp. *filicaulis*, from the lower Olifants River Valley (*Goldblatt 5666*) and from northern Namaqualand (*Goldblatt 5761*). Satellites, seen only in the latter population, are located on the metacentric pair.

The karyotype previously published for subsp. *filicaulis* (Goldblatt, 1971: 348), also $2n = 12$, corresponds to none of those described above. It has one large metacentric pair, four submetacentric pairs, and an acrocentric pair. The highest number recorded for the subspecies is presumed to be basic, $x = 9$.

MORPHOLOGY

PATTERNS OF VARIATION

The characters that unite the taxa of the *Moraea fugax* complex are: (1) the tendency for the branches to be clustered at the insertion of the leaf or leaves due to the typically short internodes above the leaves, (2) the elongate basal internode so that the leaf is usually inserted well above ground, and (3) a strongly beaked capsule.

In *Moraea gracilenta* the branches form an open system, and in *M. macrocarpa* the stem is often very short and reaches only shortly above ground level at flowering time, elongating somewhat in fruit.

Excluding the peculiarities noted above for *Moraea gracilenta* and *M. macrocarpa*, variation within the section is largely restricted to size, relative proportion of characters (Table 3), and flower color, discussed further below. The tendency for production of either one or two leaves is conspicuous in *M. fugax*. Plants from most populations of subsp. *filicaulis* have two filiform leaves. Some white-flowered populations of subsp. *fugax* have either one or two equal or unequal, linear, channeled leaves.

Plant and flower size, and color are particularly variable in *M. fugax*, and the variation is sometimes correlated with chromosome variation. Races are not sufficiently separable on either morphological or cytological grounds to make an extensive infraspecific classification desirable, and only the consistently smaller Namaqualand and northwest Cape forms with $2n = 18$, 12, or 10 seem to merit subspecific recognition. Even in this subspecies the degree of chromosomal variation is unusual, and five of the six populations studied can be distinguished by major differences in their karyotypes. Nevertheless, these populations probably have a common ancestry and merit taxonomic recognition.

Plant size. Populations fall roughly into two categories (Table 3): either robust and large-flowered with spathes (3.5–)4–6 cm long and outer tepals 2.7–4 cm long (only forms of subsp. *fugax*) or dwarf and small-flowered spathes 2–3.5(–4) cm long and outer tepals 2–2.6(–3.1) cm long. Flower and spathe size are good indications of overall plant size, because most other characters are similarly proportioned. *Moraea gracilenta* is

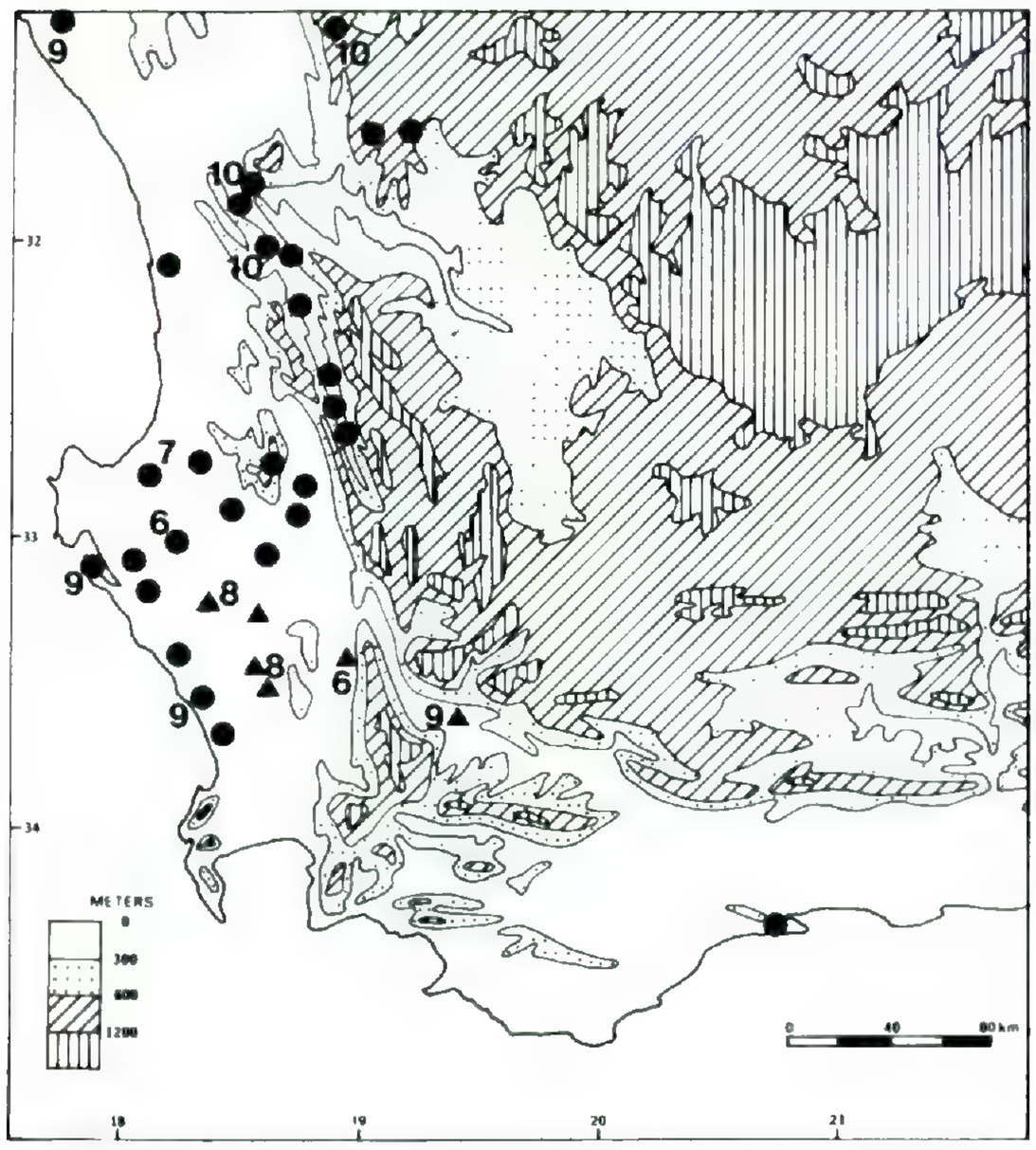
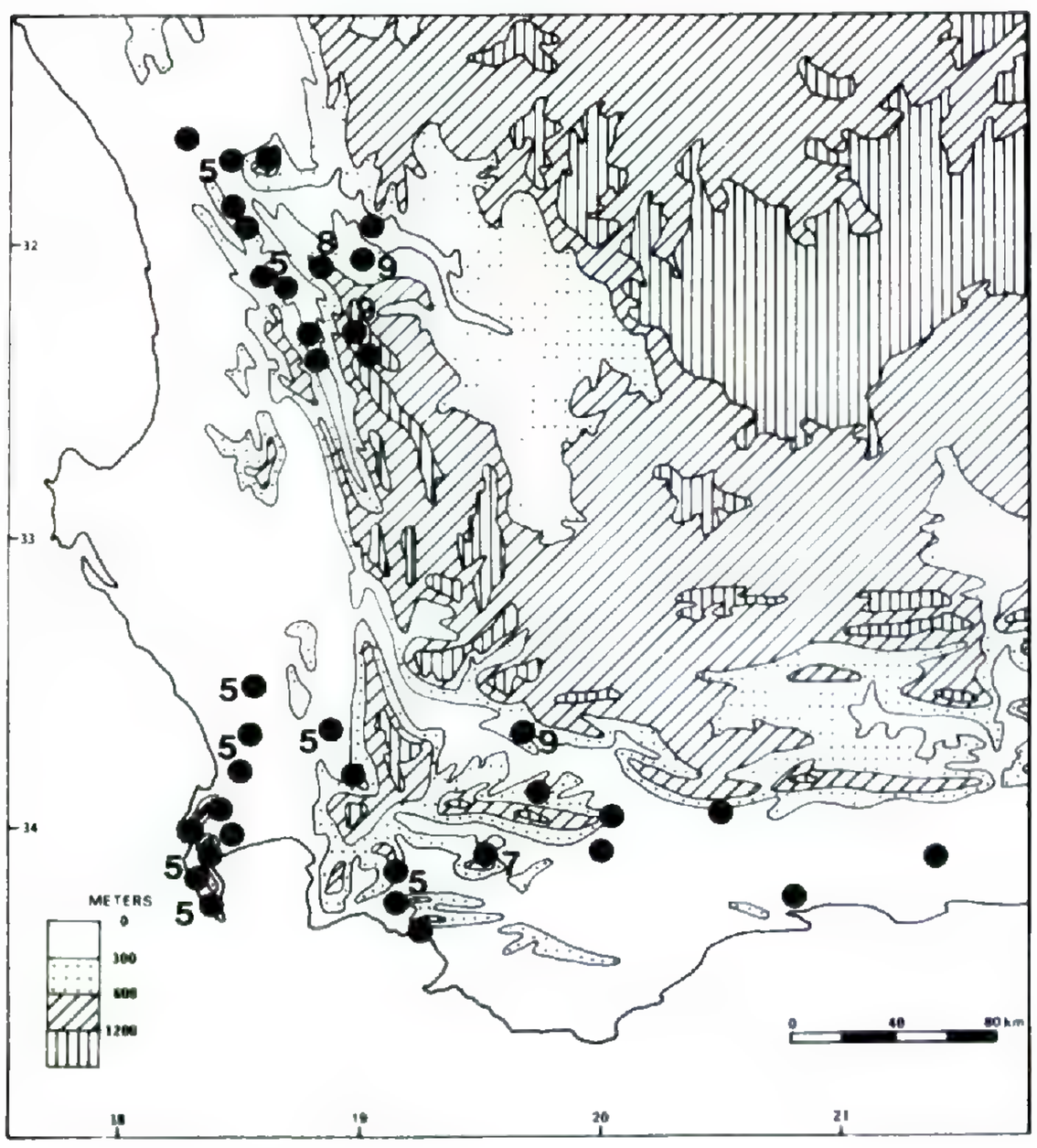


FIGURE 3. Geographical distribution of the white-flowered form of *Moraea fugax* subsp. *fugax*; circles indicate the large-flowered form and triangles the small-flowered form. Haploid numbers are indicated for populations where known. Scale = 10 μm.

exceptional is having small flowers and spathes, but the plants are usually very tall, robust, and many branched.

The two dwarf taxa, *Moraea macrocarpa* and *M. fugax* subsp. *filicaulis*, are similar at first examination but can be distinguished readily by their capsules. Those of *Moraea macrocarpa* are disproportionately long, (18–)20–25 mm, but they have sessile to subsessile spathes and single leaves. In contrast, *M. fugax* subsp. *filicaulis* has short capsules, 10–13(–15) mm long, stalked spathes, and usually two (occasionally one) filiform leaves.

The largest flowers are found in the two-leaved white-flowered form (Fig. 6A) of subsp. *fugax* (n = 10, 9, 7, 6), and individuals may be up to 60 cm high or more and have tepals 3–4 cm long. However, size is variable and forms with yellow or blue flowers have tepals that overlap in size in the lower part of the range for the white form. Thus size is insufficient to define or recognize any of the major forms of the subspecies. Subspecies *filicaulis* (Fig. 6B) has consistently small tepals (usually 2–2.5 cm long), and it often can be recognized by this characteristic alone. The small tepals are, however, correlated with small capsules and filiform leaves that in combination make confusion with subsp. *fugax* unlikely. The overlap in the size of individual characters of the two subspecies of *Moraea fugax* is part of the



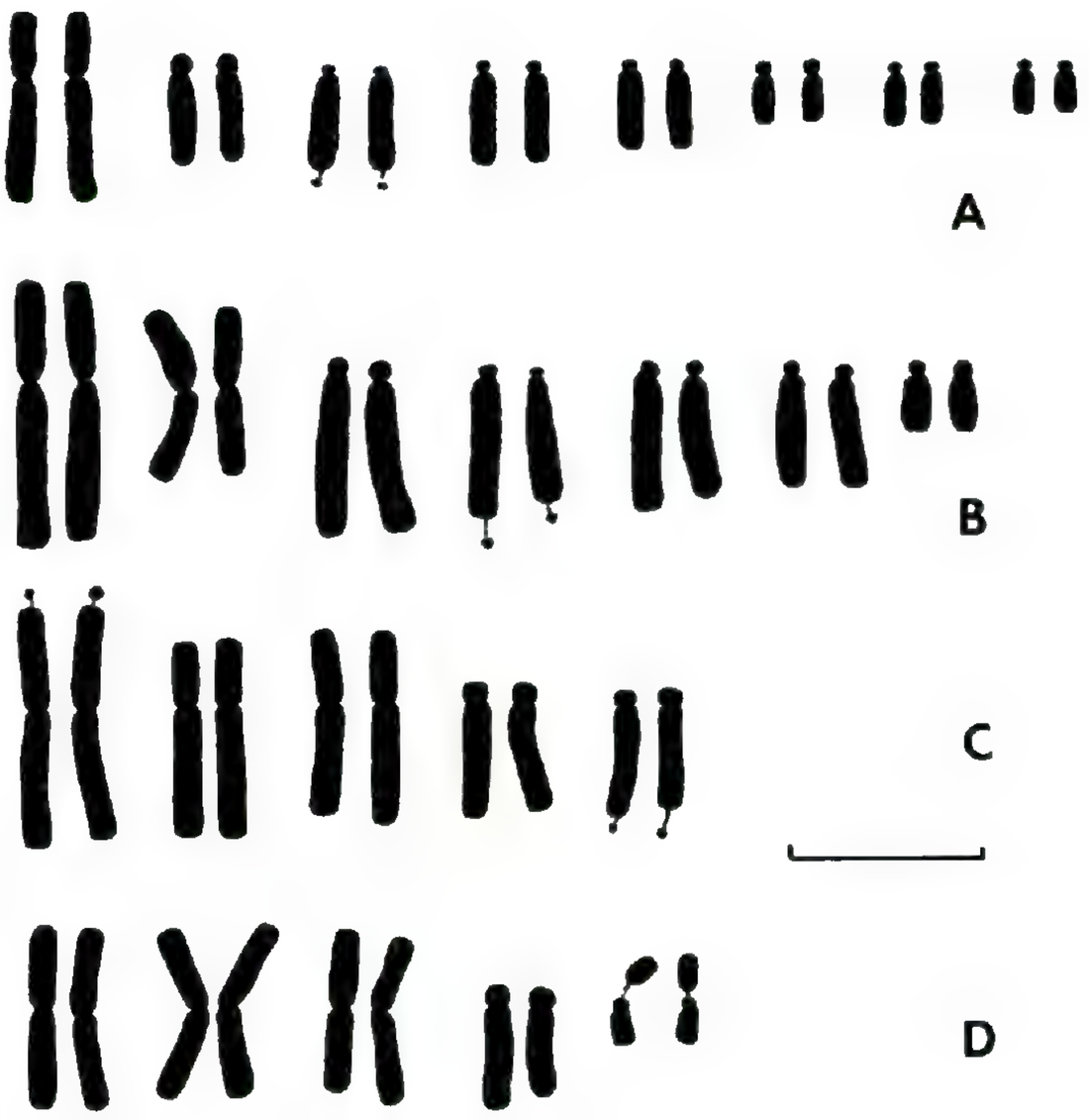
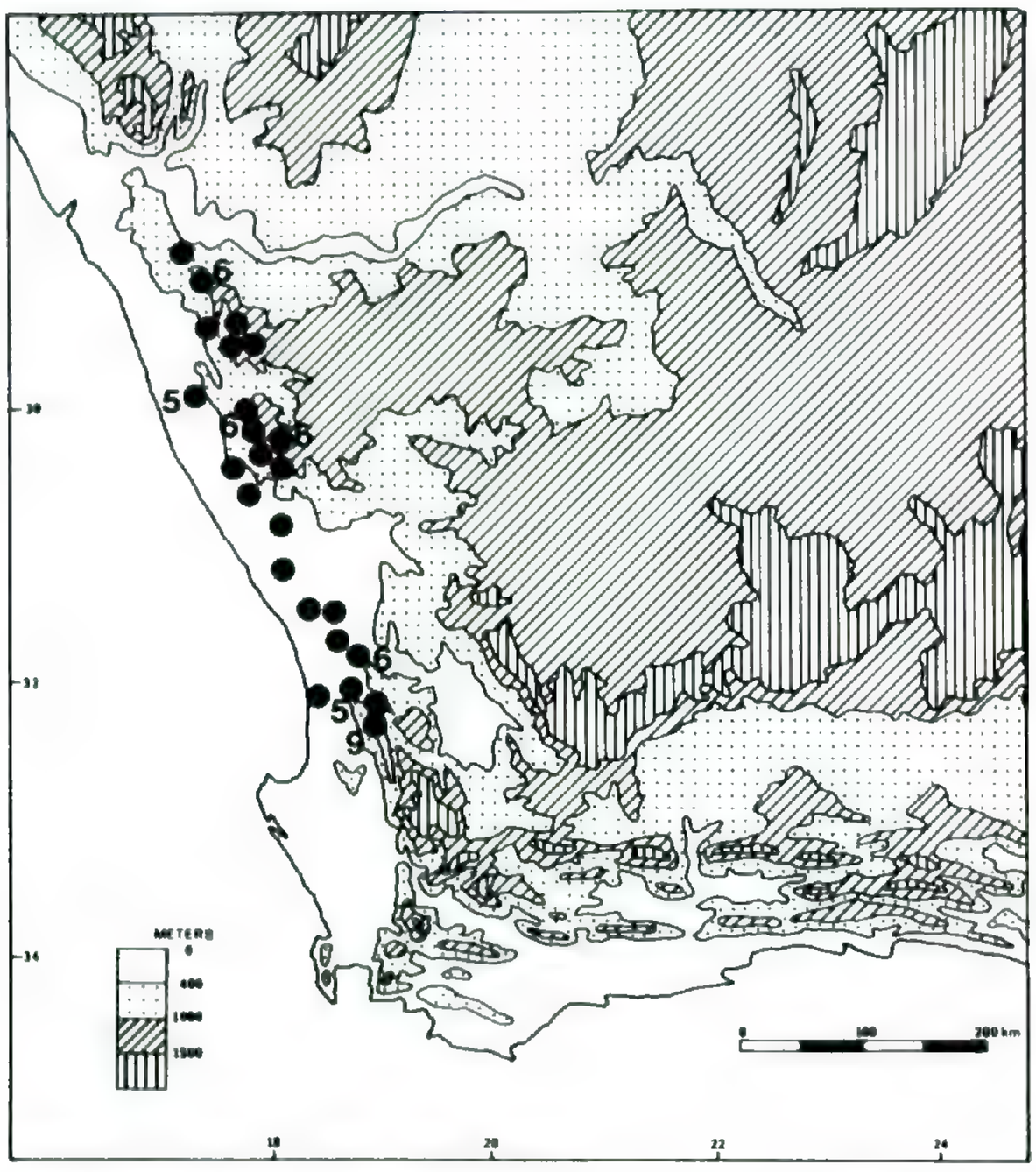


FIGURE 4. Mitotic chromosomes and geographical distribution of the yellow-flowered form of *Moraea fugax* subsp. *fugax*.—A. Pakhuis Pass, n = 8.—B. Caledon Swartberg, n = 7.—C. Foot of Houw Hoek Pass, n = 5.—D. Near Clanwilliam, n = 5. Haploid numbers are indicated for populations where known. Scale = 10 μm.



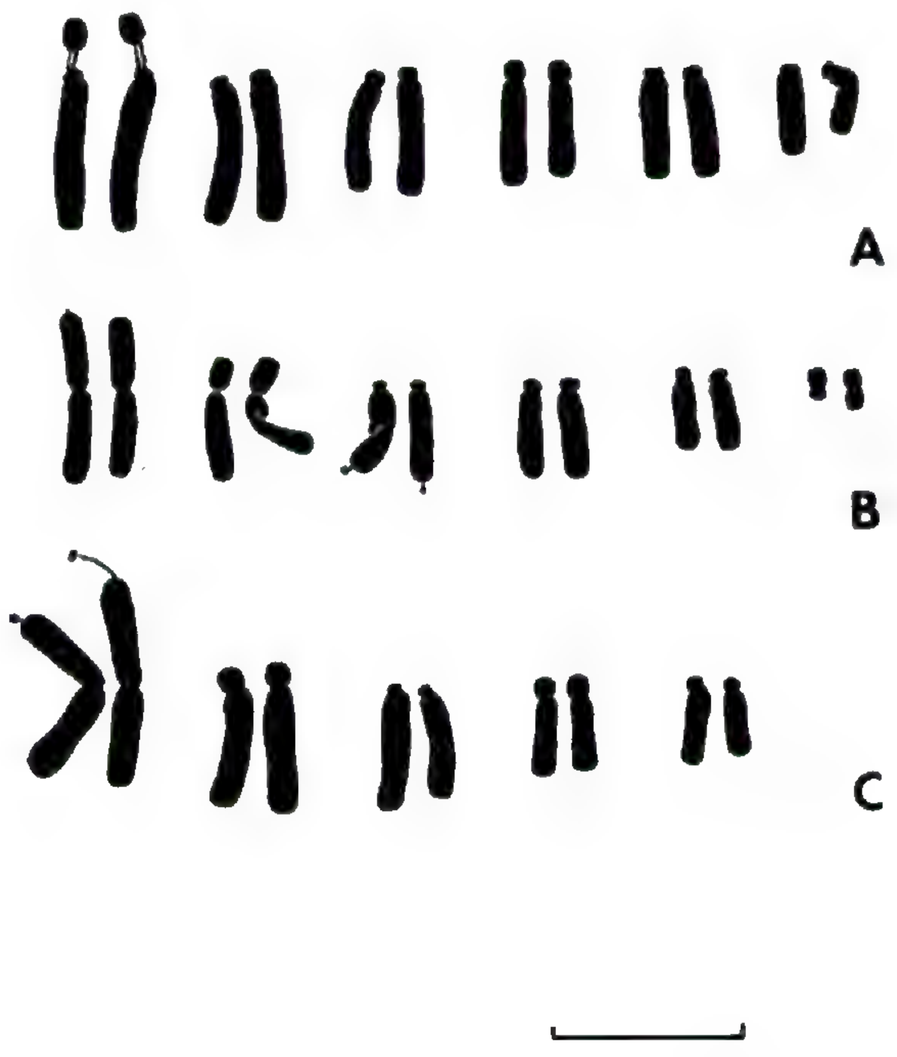


FIGURE 5. Mitotic chromosomes and geographical distribution of *Moraea fugax* subsp. *filicaulis*.—A. Near Kamieskroon, $n = 6$.—B. Eksteenfontein road, Richtersveld, $n = 6$.—C. Below Wildepaardehoek Pass, $n = 5$. Haploid numbers are indicated for populations where known. Scale = 10 μm.

reason for treating them as subspecies rather than as separate species. In some instances determinations may be arbitrary either because the plants in question are poorly grown or poorly pressed, or the plants may be truly intermediate in more than one characteristic.

Flower color. Blue-purple flowers are characteristic of all populations of *M. gracilenta* and *M. macrocarpa* but are less common in *Moraea fugax*. In the Kamiesberg, populations of subsp. *filicaulis* (corresponding exactly to the type of *M. filicaulis*) have deep blue-purple flowers, but elsewhere the subspecies has white to cream flowers, sometimes flushed pink or yellow. In subsp. *fugax*, blue to purple flowers occur in the Piketberg area and from Malmesbury south to the Cape Peninsula where they bloom later than yellow- or white-flowered populations. Chromosome numbers in this form are $n = 6$ and $n = 7$ (Fig. 2F, G), the latter found in only one population.

White-flowered populations of subsp. *fugax* are most common along the west coast (Fig. 3) and extend from just north of the Cape Peninsula to northern Namaqualand. Chromosome numbers are $n = 10$, 9, 7, and 6, the latter two numbers infrequent. In the Olifants River Valley, white-flowered populations alternate with yellow-flowered populations, the latter consistently differing in having erect inner tepals (and $n = 5$). Occasionally there is a trend for white flowers to be replaced gradually over some distance by blue ones. Populations with smaller white flowers and narrow tepals occur in the Malmesbury district and in the Breede River Valley (Fig. 3). These have $n = 9$, 8, or 6. They appear to comprise a separate white-flowered race in which aneuploid reduction has occurred independently.

Yellow-flowered forms are most common in the southwestern Cape where the type of *Moraea fugax*, an illustration of a plant of unknown origin, was most probably collected. This southern form has $n = 5$ over much of its area (Fig. 4), but $n = 7$ is known from one population. Yellow-flowered plants in the Olifants River Valley also have $n = 5$ but have a somewhat different karyotype with the smallest chromosome pair minute and metacentric (Fig. 4D). In some of the interior mountain valleys of the western Cape, from Pakhuis Pass to Robertson, similar but more slender yellow-flowered plants have either $n = 9$ or 8. Despite the several different karyotypes found in plants with yellow flowers, there seems to be no consistent and significant morphological feature to distinguish them. It is not clear whether the karyotypically diverse yellow-flowered forms comprise a monophyletic assemblage or evolved

more than once from ancestors that most probably had white flowers.

Evolution

The cytological diversity in *Moraea* sect. *Subracemosae* is certainly without parallel in Iridaceae and is most unusual in plants generally. The section appears to be in a stage of rapid evolution with the differentiation of numerous regional and local morphological and cytological races. *Moraea fugax* is the most chromosomally variable and probably also the most morphologically variable species in *Moraea* and its close allies (Goldblatt, 1971, 1979, 1980). Other species, notably *M. tripetala* and *M. papilionacea,* are also morphologically variable and have differentiated into several distinct forms or races. In these species cytological variability is limited, as would normally be expected, although different cytotypes can be distinguished (Goldblatt, in prep.).

The chromosomal diversity in the several races of *Moraea fugax* probably has promoted population differentiation in the species by restricting hybridization and consequent recombination in forms that have differentiated cytologically. It probably played little role in the origin of population differences that most likely developed in isolation at times when more arid conditions prevailed along the Cape west coast, and the distribution of the various forms or races of the species was more restricted than at present.

It is especially remarkable that the extensive chromosomal variation has developed in several lines. The ancestor of the complex probably had small blue-purple flowers, two long leaves, and many branches in an open arrangement and most likely resembled *M. gracilenta.* This species or its immediate ancestor may have given rise to the dwarf and reduced *M. macrocarpa* and to the larger flowered form of *M. fugax,* both of which have similar karyotypes with $x = 10$.

Evolution in *Moraea fugax* presumably followed a pattern of reduction in plant size, length and number of branches, and diversification of flower color. Distinctive forms or races tend to have either fewer branches, shorter stems, or narrower tepals and often have only a single leaf, as in the type form of *M. fugax.*

The evolution of the different color forms in subsp. *fugax* was probably a significant development, although it is difficult to assess its evolutionary importance. The available data do not favor a single or multiple origin for either blue or yellow color. However, it is clear from the karyology that chromosomal diversification occurred at least once in each of the major color forms after their differentiation. Furthermore, flower color in other species of *Moraea* rarely varies within a species, so it is reasonable to postulate a single (or very few) color change events. Thus it is likely that aneuploid reduction from $n = 9$ to 5 occurred in a monophyletic yellow-flowered form of subsp. *fugax* and in the late-blooming blue-purple-flowered form at least from $n = 7$ (the highest number recorded here) to 6. The difference in karyotpes in the yellow-flowered forms with $n = 5$ from the southwestern Cape and in the Olifants River Valley suggests either an independent origin of this number from a common ancestor with a higher haploid number or major structural change in the karyotype with $n = 5$. It also seems likely that plants with smaller white flowers and narrow tepals from the Malmesbury district and Breede River Valley comprise a regional race distinct from the large white-flowered form, and the recorded numbers of $n = 9$, 8, and 6 indicate separate aneuploid reduction series in the two white-flowered races.

Systematic Treatment

Key to the Taxa of Section *Subracemosae*

1a. Spathes short, 2–3.5(–4) cm long; capsules 8–13 rarely to 15 mm long.
  2a. Leaves filiform and usually two; branches few to several clustered; flowers opening shortly after midday ..... 3B. *M. fugax* subsp. *filicaulis*
  2b. Leaves linear, usually 2–3 mm wide, solitary; branches many and paniculate; flowers opening after 3:30 P.M. ..... 1. *M. gracilenta*

1b. Spathes longer, (3.5–)4–6.5 cm long; capsules 15–28(–40) mm long.
  3a. Flowers small, the outer tepals 2–3 cm long; capsules at least 18 mm long; branches solitary or two to three and sessile to subsessile ..... 2. *M. macrocarpa*
  3b. Flowers large, the outer tepals 2.7–4 cm long; capsules 15–28(–40) mm long; branches usually several and stalked ..... 3A. *M. fugax* subsp. *fugax*

1. **Moraea gracilenta** Goldbl., Ann. Missouri Bot. Gard. 63: 724. 1976 [1977]; Fl. Pl. Africa 44: tab. 1748. 1977. TYPE: South Africa. Cape: sandy flats S of Piekenierskloof Pass, Piketberg district, *Goldblatt 3279* (holotype, MO; isotypes, K, NBG, PRE, S). FIGURE 6A.

FIGURE 6. Morphology of *Moraea gracilenta* (A) and *M. macrocarpa* (B). Habits ×0.5; flowers, and floral details life size.

Moraea edulis L. f. var. *gracilis* Baker, Handb. Irid. 56. 1892; Fl. Cap. 6: 21. 1896. TYPE: South Africa. Cape: Tulbagh Kloof to Piekeniers Kloof, *Zeyher 1647* [lectotype, K, designated by Goldblatt (1976b); isolectotypes, PRE, S].

Plants 30–80 cm high, many branched. *Corm* 1.5–2 cm diam., deeply buried to 25 cm; tunics of fine to medium pale fibers. *Leaf* solitary, canaliculate, linear, exceeding the inflorescence but usually trailing, inserted well above the ground at the base of the first branch. *Stem* erect and multibranched. *Spathes* herbaceous, becoming dry, the apices brown, acute; inner spathe 2.5–3.5(–4) cm long, the outer less than half the inner. *Flower* pale blue-mauve, strongly scented; *outer tepals* 2–3 cm long, 6–8 mm at the widest point, lanceolate; *inner tepals* 1.8–2.8 cm long, 5–6 mm wide, spreading. *Filaments* ca. 5 mm long, united in the lower half; *anthers* 4–6 mm long, white. Ovary 8–10 mm long, included in the spathes, *style branches* 7–9 mm long, crests linear-lan-

ceolate, 7–12 mm long. *Capsule* 8–12 mm long. *Chromosome number* $2n = 20$.

Flowering time. Late September to November, extending to December at higher altitudes; flowers opening after 3:30 P.M. sometimes as late as 5 P.M. and fading by 7 P.M.

Distribution. Western coastal belt from Tulbagh Kloof to Clanwilliam, in sandy flat areas, near streams or at the foot of mountains. Figure 1.

Moraea gracilenta differs consistently from all the forms of the variable *M. fugax* in its open and many branched habit, small blue flowers, and short inflorescence spathes and capsules. Its floral phenology is also markedly different from that of *M. fugax.* Blooming occurs in the same months, and the flowers of both species last only a day, but while those of *M. gracilenta* open between 3:30 and 5 P.M. and last until at least 7 P.M., the flowers of *M. fugax* open at about midday and are usually completely wilted by 6 P.M. The difference in phenology has been observed on several occasions in wild populations and appears to vary little. *Moraea gracilenta* is apparently pollinated by small moths, which I have seen visiting the pale, sweetly scented flowers as they open in the late afternoon.

Specimens examined. SOUTH AFRICA. CAPE: 32.18 (Clanwilliam) riverbank near Clanwilliam (BB), *Goldblatt 3076* (MO), *Galpin 11482* (B, K, PRE); Eendekuil (DB), *Loubser 851* (NBG); sandy areas between Eendekuil and Piekenierskloof Pass, *Goldblatt 3279* (K, MO, NBG, PRE, S), *3029* (MO, NBG, PRE).

32.19 (Wuppertal) near Warm Baths, Olifants River Valley (CA), *L. Bolus s.n.* (BOL-20323, K, PRE); Citrusdal, riverbank at campsite, *Goldblatt 6557* (MO, PRE), *6708* (MO); sandy alluvium near river at the entrance to the old Elandskloof Pass, *Goldblatt 7122* (MO, PRE); Elandskloof, *Compton 16748* (NBG).

33.19 (Worcester) Tulbagh Kloof to Piekenierskloof (AC), *Zeyher 1647* (K, PRE, S); Tulbagh Kloof, *Compton 12399* (NBG), *Ecklon & Zeyher Irid. 23* (77.9) (MO, P, S); Gydo (AD), *Leipoldt 3004* (BOL, K, PRE).

2. Moraea macrocarpa Goldbl., sp. nov. TYPE: South Africa. Cape: S of Redelinghuys, Piketberg district, *Acocks 24359* (holotype, PRE; isotype, MO). FIGURE 6B.

Plantae 30–80 cm altae, ramis 1–3, cormo 8–12 mm diam., folio solitario tereti ad lineari-filiformi, spathis interioribus 4–5(–6.5) cm longis, exterioribus parvioribus, floribus caeruleis, tepalis exterioribus 2–3 cm longis, filamentis 5–6 mm longis, capsulis (18–)20–25 mm longis.

Plants 30–80 cm high, simple or few-branched. *Corm* 8–12 mm diam.; tunics of fine pale fibers. *Leaf* solitary, canaliculate, terete to linear-filiform, 0.4–1.5 mm wide, erect, much longer than the spathes, inserted near, to well above the ground. *Stem* erect, filiform, simple or with two (to three) sessile or subsessile inflorescences. *Spathes* herbaceous, becoming dry above, the apices brown, acute, the inner (3.4–)4–5(–6.5) cm long, the outer about one-third as long as the inner. *Flower* blue-mauve, with yellow nectar guides, the claws of the outer tepals yellow with dark spots, scented; *outer tepals* 2–3 cm long, 7–10 mm at the widest, lanceolate; *inner tepals* 1.8–2.8 cm long, 5–7 mm wide, spreading. *Filaments* 5–6 mm long, united in the lower half; *anthers* 4–5 mm long, white. Ovary 17–21 mm long, included in the spathes, *style branches* 6–7 mm long, the crests linear-lanceolate, 12–18 mm long. *Capsule* cylindric, (18–)20–25 mm long. *Chromosome number* $2n = 20$.

Flowering time. (May–)August to early October; flowers opening soon after midday and fading at about 5 P.M.

Distribution. West coast from Hopefield to the Olifants River mouth and locally in the Breede River Valley, in deep white sand. Figure 1.

Moraea macrocarpa has been associated with *M. fugax* until now, or it has been confused with *M. filicaulis,* now *M. fugax* subsp. *filicaulis.* It bears a superficial resemblance to the latter in its slender stem, small corm, and small flower. Cytological study has, however, provided evidence that they are unrelated. *Moraea macrocarpa* has $2n = 20$, the basal diploid number for sect. *Subracemosae,* while *M. fugax* subsp. *filicaulis* has $2n = 18$, 12, and 10. The difference suggests that they may be derived from different ancestral stock, and the several differences between *M. macrocarpa* and *M. fugax* subsp. *filicaulis* are significant.

The differences between *Moraea macrocarpa* and *M. fugax* subsp. *filicaulis* include spathe, ovary and capsule length, and leaf number. The majority of specimens that I have examined of subsp. *filicaulis* have two leaves while *M. macrocarpa* has only one. The capsules of *M. macrocarpa,* its most striking attribute, are disproportionately long for the small plants and are in the 20–25 mm range. The ovary and the spathes are correspondingly long because the capsule remains enclosed in the spathes throughout development. The latter range from 4–6.5 mm long. In subsp. *filicaulis* the capsules are only 8–13

(–15) mm long and the spathes 2–3.5(–4) mm long. The flowering stem of subsp. *filicaulis* is typically branched, and the branches are usually distinctly stalked. In contrast the flowering stems of *M. macrocarpa* usually have only a single terminal inflorescence, rarely one to two branches, and the branches are more or less sessile.

Moraea macrocarpa occurs along the Cape west coast from Hopefield to Trawal in the Olifants River Valley and locally in the interior in the Breede River Valley near Worcester. It grows in deep, coarse-grained sand. Occasionally it occurs with the taller and more robust *M. fugax* subsp. *fugax*. Its range overlaps slightly that of *M. fugax* subsp. *filicaulis* in the Olifants River Valley but they have not been observed growing together.

Specimens examined. SOUTH AFRICA. CAPE: 31.18 (Vanrhynsdorp) mountains W of Trawal, in sand (DC), *Goldblatt 5661* (MO).

32.18 (Clanwilliam) 2 km N of the Lamberts Bay road towards Vredendal (AB), *Nordenstam & Lundgren 1552* (MO, S); between Graafwater and Lamberts Bay (AB-BA), *L. Bolus s.n.* (BOL 23193); between Elandskloof and Clanwilliam (?BC), *Leipoldt s.n.* (BOL 20950); Alexandershoek (BD), *Schlechter 5149* (BOL, GRA); 11.7 mi. S of Redelinghuys, white sand (DA), *Acocks 24359* (MO, PRE); 9.5 mi. SW of Redelinghuys, *Acocks 19689* (K); near Sauer, Piketberg (DD), *Barker 2687* (NBG).

32.19 (Wuppertal) Pakhuis Pass (AA), *Barker 1999* (NBG), *Compton 9798* (NBG).

33.18 (Cape Town) Oosterwal, Hopefield (?AB), *Pamphlett 89* (NBG); in planitie prope Darling (AD), *H. Bolus 12833* (BOL, K).

33.19 (Worcester) Aan de Doorns, farm Reiers Rus, along the Breede River (CB), *Goldblatt 6961* (MO, NBG).

3. Moraea fugax (de la Roche) Jacq., Hort. Bot. Vindob. 3: 14. tab. 20. 1776; Goldblatt, J. S. African Bot. 36: 316. 1970; Ann. Missouri Bot. Gard. 63: 725. 1976 [1977]. *Vieusseuxia fugax* de la Roche, Descr. Pl. Aliq. Nov. 33. 1766. TYPE: Illustration in van Hazen, Cat. Arb. & Pl. 67. 1759 (lectotype designated by Goldblatt, 1970). FIGURE 7.

(For additional synonyms see under the subspecies.)

Plants medium to large, 12–40(–50) cm high, branched. *Corm* (1–)1.5–3 cm diam.; tunics usually pale, rarely dark, of fine to medium fibers. *Cataphylls* usually two, membranous, pale, becoming dry and brownish and often broken above. *Leaf* solitary or two, equal or unequal in length, subopposite, inserted well above ground immediately below the first branch, canaliculate, usually much exceeding the stem and trailing, occasionally loosely twisted distally. *Stem* erect or more often somewhat inclined, with a conspicuous, long lower internode, the branches crowded, occasionally subracemose. *Spathes* herbaceous, becoming dry, the upper margin light brown, apices attenuate; inner spathe (2–)2.5–6 (–8) cm long, the outer one-half to two-thirds as long as the inner. *Flowers* white, blue, or yellow, strongly scented; *tepals* lanceolate, the limb more or less equal to the claw, the limb spreading horizontally or the inner occasionally erect, outer 2–4 cm long, inner 2–3.5 cm long, 5–8 mm wide. *Filaments* 5–10 mm long, united in the lower half; *anthers* 4–10 mm long. Ovary 8–20 mm long, included in the spathes, *style branches* 1.5–2 cm long, the crests lanceolate 6–18 mm long. *Capsule* oblong to cylindric, distinctly beaked, 9–28(–40) mm long. *Chromosome number* $2n$ = 20, 18, 16, 14, 12, 10.

Flowering time. August to October, occasionally extending into December at high elevations.

Distribution. Northern Namaqualand to the southern Cape, typically in deep sandy or rocky sandstone or granitic soil. Figure 1.

As circumscribed here, *Moraea fugax* is an unusually variable species with several distinct forms or races. Of these only a series of dwarf, small-flowered and usually two-leafed populations, described in the past as separate species, *M. filicaulis* and *M. diphylla*, are given taxonomic recognition as subsp. *filicaulis*. This subspecies occurs throughout Namaqualand and extends south to the Clanwilliam district. Although subsp. *filicaulis* is itself somewhat variable, it appears to constitute a natural assemblage, united by its slender stem, filiform leaves, relatively small flower with tepals 2–2.6(–3.5) mm long and especially small capsules (10–15 mm long). Subspecies *filicaulis* apparently has $x = 9$. Some cytological variation is evident in karyotypes from several localities, and derived numbers of $n = 6$ and 5 have been recorded.

The pattern of variation is more complex in subsp. *fugax*, the several forms of which are united by their large size, long broad leaves, and relatively large flowers with tepals 23–40 mm long and capsules 15–40 mm long. Chromosomal variation is particularly extensive in this subspecies with numbers ranging from $2n = 20$ to 10. The variation within subsp. *fugax* is discussed in detail after the subspecies description.

KEY TO THE SUBSPECIES

1a. Spathes short, 2–3.5(–4) cm long; capsules 9–13 rarely to 15 mm long; flowers small to medium, the outer tepals 2–2.6(–3.5) cm long; leaves filiform and usually two; branches clustered ..... 3B. subsp. *filicaulis*

1b. Spathes long, (3.5–)4–6.5 cm long; capsules 15–28(–40) mm long; flowers medium to large, the outer tepals 2.7–4 cm long; leaves channeled, linear, either one or two; branches usually clustered but sometimes subracemose ..... 3A. subsp. *fugax*

3A. M. fugax subsp. fugax. FIGURE 7A.

Iris edulis L. f., Suppl. Pl. 93. 1781; *Moraea edulis* (L. f.) Ker, Bot. Mag. 17: tab. 613. 1803; Baker, Fl. Cap. 6: 20. 1896; *Vieusseuxia edulis* (L. f.) Link, Enum. Hort. Berol. Alt. 1: 56. 1821. TYPE: South Africa. Cape: exact locality uncertain, *Thunberg s.n.* [lectotype, Herb. Thunb. 1123 (UPS), designated by Goldblatt, 1976b].

Moraea corniculata Lam., Tabl. Encycl. 1: 114. 1791; Encycl. 4: 227. 1797. TYPE: South Africa. Cape, *Sonnerat s.n.* (lectotype, P, designated by Goldblatt, 1976b).

Iris longifolia Schneev., Icon. Pl. Rar. 7: tab. 20. 1792; *Moraea longifolia* (Schneev.) Sweet, Hort. Brit., ed. 2, 496. 1830, nom. illeg., non *M. longifolia* (Jacq) Pers. (1805). TYPE: South Africa. Cape: without precise locality (lectotype, illustration in Schneev., Icon. Pl. Rar. 7: tab. 20. 1792, designated by Goldblatt, 1976b).

Moraea odora Salisb., Parad. Lond. 1: tab. 10. 1805. TYPE: Illustration in Salisb., Parad. Lond. 1: tab. 10. 1805 (lectotype designated by Goldblatt, 1976b).

Plants medium to large, 12–40(–50) cm high, branched. *Corm* (1–)1.5–3 cm diam.; tunics usually pale, rarely dark, of fine to medium fibers. *Leaf* usually solitary, occasionally two, equal or unequal in length, canaliculate, usually much exceeding the stem and trailing. *Stem* sturdy, 2–3 mm thick. *Inner spathe* 4–8 cm long, the outer ca. one-third the length of the inner. *Flowers* white, blue, or yellow, strongly scented; *outer tepals* 2.3–4 cm long, lanceolate, the limb more or less equal the claw; *inner tepals* 2–3.5 cm long, erect or slight reflexed, 5–8 mm wide. *Filaments* 6–10 mm long; *anthers* 4–8 mm long. Ovary 14–20 mm long, *style branches* 1.5–2 cm long, the crests lanceolate, 10–18 mm long. *Capsule* clavate to cylindrical, distinctly beaked, 1.5–2.8(–4) cm long; *seeds* many, angled. *Chromosome number* $2n = 20, 18, 16, 14, 12, 10$.

Flowering time. August to November, extending into December at higher elevations.

Distribution. Namaqualand to the southern Cape, frequently in sandy situations. Figures 1, 3, 4.

Variation. Plants corresponding to the type of *Moraea fugax* have large, yellow flowers, a single leaf, and are of generally moderate size with an umbellate branching pattern (although tall racemosely branching plants may occur). Populations of this form occur in the south of the range of subsp. *fugax* and extend from south of Malmesbury to the Cape Peninsula and east to Robertson and Swellendam. The most frequent karyotype (Fig. 4) has $n = 5$, but in the east of its range, at Swartrivier, north of Caledon Zwartberg, plants have $n = 7$. Similar but more slender yellow-flowered populations in the interior near Robertson and to the north in the Cedarberg at Brandewyn River and Algeria have $n = 9$, and a population in Pakhuis Pass has $n = 8$. Despite this range of karyotypes, there seem to be no morphological features that distinguish the cytotypes. A yellow-flowered form from the Olifants River Valley and adjacent valleys is similar to yellow-flowered plants that occur to the south except that they consistently have erect inner tepals. These plants also have $n = 5$ but have a somewhat different karyotype from the southern form that has the same number.

A second form that occurs in the southern part of the range of subsp. *fugax* has deep blue flowers, is relatively tall, and is late blooming. On the Cape Peninsula and the Cape Flats the yellow-flowered form, described above, blooms in August and September, while the blue-flowered form blooms only in October or later, and flowering plants have been collected as late as January. Populations of this form usually have $n = 6$, but $n = 7$ was found in a population near Cape Point. This form is not well sampled.

Along the west coast from near Malmesbury as far north as Hondeklipbaai in Namaqualand (Fig. 3), there is a large, white-flowered form of the species corresponding to Baker's *Moraea edulis* var. *longifolia*. It is generally tall and racemosely branched. This robust form also occurs in the Olifants River Valley. Most populations have $n = 10$ or 9, but $n = 7$ and 6 are found in the Velddrif and Hopefield areas (Goldblatt, 1971: 348; Fig. 2E).

In the Malmesbury district there is a distinctive white-flowered form that has relatively large flowers with unusually narrow tepals. Populations around Malmesbury and to the north towards Hopefield have $n = 8$, but plants corre-

FIGURE 7. Morphology of *Moraea fugax*.—A. Subsp. *fugax*, large white-flowered form.—B. Subsp. *filicaulis*. Habits ×0.5; flowers life size.

sponding to this form from south near Gouda have $n = 6$. In the Breede River Valley similar plants have $n = 9$ (Fig. 3).

There is no recorded intrapopulational variation for flower color. Occasionally there is a trend for white flowers to be replaced gradually over some distance by blue ones as in the Piketberg district. In the Olifants River Valley pop-

ulations of white- or yellow-flowered plants alternate over distances of several kilometers without any clear pattern. The yellow-flowered populations consistently differ in having erect inner tepals and as far as is known, $n = 5$.

History. *Moraea fugax* is typified by an illustration of a yellow-flowered plant of unknown origin, most probably collected on or near the Cape Peninsula. It was cultivated in Holland in the mid-seventeenth century and figured in the 1759 "Catalogue des Arbores et Plantes" of the van Hazen, Vakinburg & Company Nursery. The plant was described by Daniel de la Roche in 1766 and the illustration in van Hazen's Catalogue is assumed to be the type. *Moraea fugax* was first assigned to the genus *Vieusseuxia* but was transferred to *Moraea* by Jacquin in 1776, who figured the blue-purple-flowered form of subsp. *fugax* but considered it conspecific with plants with yellow flowers. Subsequently, other forms of subsp. *fugax* were described from plants in cultivation in Europe, notably *M. longifolia* (as *Iris*) by Schneevoogt in 1792 and *M. odora* by Salisbury in 1805. Both these species represent the robust white-flowered form of subsp. *fugax*.

Specimens examined. SOUTH AFRICA. CAPE: 29.17 (Springbok) Komaggas (CD), *Maguire 403* (NBG).

30.17 (Hondeklipbaai) near Soebatsfontein (BA), *van Berkel 268* (NBG).

30.18 (Kamiesberg) Eenkokerboom, in collibus' (CC), *Schlechter 11063* (MO, P).

31.18 (Van Rhynsdorp) Vredendal commonage (CB-DA), *Hall 3844* (NBG, PRE, STE), *Bayliss 6126* (MO); Nardouw Pass, *Lewis s.n.* (BOL-22205); top of Gifberg (DC), *Bayliss 6161* (MO); W of Klawer, below the Winterhoekberg, *Goldblatt 5778* (MO); slope above the Olifants River at the bridge near Klawer, *Goldblatt 2828* (MO); 5 km S of Trawal, Olifants River Valley, *Goldblatt 5792* (MO); hills W of Trawal on the road to Kleipan, *Goldblatt 5667* (MO).

31.19 (Calvinia) sandy places near Nieuwoudtville (AC), *Galpin 11128* (K, PRE); near Nieuwoudtville, *Buhr s.n.* (Nat. Bot. Gard. 639/29 in BOL), *Goldblatt 5843* (MO); Doornbosch (CC), *Hall 3881* (NBG, STE); top of Botterkloof (CD), *van Niekerk 3197* (BOL), *Hall 3876* (NBG); farm Soutpan, ca. 42 km SE of Nieuwoudtville, *Goldblatt 7080* (MO).

32.18 (Clanwilliam) sandy slope N of Clanwilliam facing the Olifants River (BB), *Goldblatt 5936* (MO); between Clanwilliam and Graafwater, *Goldblatt 5161* (MO); sandveld near Velddrif (CC), *van Jaarsveld s.n.* (MO); hills NW of Moutons Vlei (DC), *Pillans 7398* (BOL); Piketberg (DD), *Compton 22989* (NBG), *H. Bolus s.n.* (MO); N of Piketberg towards Piekenierskloof, *Goldblatt 5676* (MO).

32.19 (Wuppertal) Cedarberg Pass near Algeria (AC), *Goldblatt 3250* (MO); Cedarberg at Algeria, *Viviers s.n.* (MO).

33.18 (Cape Town) Langebaan (AA), *Lewis s.n.* (BOL); between Hopefield and Langebaan, *L. Bolus s.n.* (BOL-20339, K); near Hopefield, *Marloth 8207* (PRE); Groenekloof (AD), *Zeyher 1646* (K, PRE, S); road to Bokbaai, *Goldblatt 5850* (MO); 20 km NW of Malmesbury on the road to Hopefield (BB), *Goldblatt 4081* (MO); Malmesbury (BC), *Barker 2554* (NBG), *Goldblatt 4813* (MO); 8 km N of Malmesbury, *Goldblatt 3025* (MO, NBG, PRE); sandy slopes S of Malmesbury opposite Abbotsdale, *Goldblatt 5116* (MO); slopes of Koeberg N of Cape Town (DA), *Goldblatt 4080* (MO); near Sea Point, Cape Town (CD), *Wolley Dod 1611* (BOL); Wynberg Hill, *Pillans 1950* (MO); Kirstenbosch, *Barker 2066* (BOL), *Verdoorn s.n.* (PRE); Table Mountain, *Ecklon 823* (PRE-11149).

33.19 (Worcester) hills near Saron (AA), *Schlechter 10605* (BR, K, MO, PRE, S); foot of the Elandsrivier Mts. on the farm Elandsberg (AC), *Goldblatt 5851* (MO); Michells Pass (AD), *Schlechter 8966* (GRA); Aan de Doorns, farm Reiers Rus, near Moordkuil (CB), *Goldblatt & Snijman 6962* (MO); near French Hoek (CC), *Gillett 1830, 1831* (STE); 15 km from MacGregor on Bonnievale road (DD), *Marsh 806* (PRE, STE); hills above Goree, S of the Robertson–Ashton road, *Goldblatt 5860* (MO).

34.18 (Simonstown) beyond Simonstown (AB), *Wolley Dod 505* (BOL, K); Fish Hoek, *Wolley Dod 1633* (BOL, K); burned lower slopes of Klaasjagersberg, opposite Cape Point Reserve, *Goldblatt 5264* (MO); Silvermine road just N of the Noordhoek turnoff, *Goldblatt 5154* (MO); Olifants Bos (AD), *Barker 3876* (BOL, NBG); Smitswinkel, Cape Peninsula, *Walgate 433* (NBG); Cape Reserve, S of Sirkels Vlei, *Goldblatt 5403* (MO); Strandfontein (BA), *Rycroft 2371* (MO); dunes near Strand (BB), *Parker 4141* (BOL, K).

34.19 (Caledon) burned flats at the foot of Houw Hoek Pass (AA), *Goldblatt 4292* (MO); Caledon (AB), *Gillett 1111* (STE); N side of Caledon Swartberg, *Goldblatt 5782* (MO); Onrust River (AC), *Van Niekerk 300* (BOL); Mainstay, Onrus River, *Robertson 111* (MO); roadside ca. 10 km S of Bot River, *Goldblatt 2997* (MO); Die Duine, Hermanus, stabilized sand dunes, 50 m (AD), *Williams 1010* (MO, PRE, US, WAG).

34.20 (Bredasdorp) near Storms Vlei (AA), *Goldblatt 2923* (MO, PRE); 14 km E of Swellendam (BA), *Story 3090* (PRE); Cape Infanta (BD), *Blum 64* (E), *214* (E); Zoetendals Vlei (CA), *Leipoldt 3559* (PRE).

34.21 *(Riversdale) Riversdale (AB), H. Bolus s.n.* (BOL).

34.22 (Mossel Bay) Mossel Bay (AA), *Burchell 6295* (K); Ruigte Vlei, near Knysna (BB), *Fourcade 1557* (BOL, GRA).

WITHOUT PRECISE LOCALITY: 'Clanwilliam, am Fluss Olifantrivier und bei Villa Brakfontein' *Ecklon & Zeyher Irid. 16* (76.10) (MO); 'Worcester, Tulbaghskloof, Tulbaghsthal, am Fuss des Winterhoeksberg' etc., *Ecklon & Zeyher Irid. 23* (77.11) (MO); 'bei Puspasvlei, Voormansbosch, Duiwelsbosch' etc., *Zeyher 4079* (70.10) (S).

3B. M. fugax subsp. **filicaulis** (Baker) Goldbl., stat. nov. *Moraea filicaulis* Baker, Handb. Irid. 56. 1892. TYPE: South Africa. Cape: Kamiesberg between Roodeberg and Ezel-

skop, *Drège 2605* (lectotype, K, designated by Goldblatt, 1976b; isolectotypes, MO, P). FIGURE 7B.

Moraea diphylla Baker, Bull. Misc. Inform. 1906: 42. 1906. TYPE: South Africa. Cape: Olifants River, *Penther 734* (lectotype, K, designated by Goldblatt, 1976b).

Plants small to medium, 6–12(–20) cm high, few to several-branched. *Corm* 7–16 mm diam.; tunics usually pale, rarely dark, of fine to medium fibers. *Leaves* usually two and subopposite, occasionally solitary, linear-filiform, channeled, 1–2 mm wide, equal or occasionally unequal in length, occasionally loosely spiraled distally. *Stem* slender, to 1 mm thick. *Inner spathe* 2–3.5(–4) cm long, the outer half to one-third as long as the inner. *Flowers* white, sometimes shaded bluish or pinkish, rarely dark blue-violet, scented, with yellow nectar guides; *tepals* lanceolate, limbs spreading horizontally, outer 2–2.6(–3.5) cm long, 0.8–12 mm wide; inner 1.8–3 cm long, 5–7 mm wide. *Filaments* 5–6 mm long; *anthers* 4–5(–6) mm long. Ovary 8–10 mm long, the *style branches* 8–10 mm long, the crests lanceolate 8–14 mm long. *Capsule* 10–13(–15) mm long. *Chromosome number* $2n = 18, 12, 10$.

Flowering time. August to October.

Distribution. Namaqualand south to the Olifants River Valley near Clanwilliam, in sandy or rocky soil. Figure 5.

Moraea fugax subsp. *filicaulis* is a small-flowered subspecies with a slender stem, small corm, and usually two filiform leaves. The subspecies ranges from northern Namaqualand to the central Olifants River Valley near Clanwilliam (Fig. 5). There are three chromosome numbers recorded in the taxon, $n = 9$ in one population, $n = 6$ in three populations, and $n = 5$ in two populations. The type form of *M. filicaulis*, from the Kamiesberg, has deep blue-purple flowers and $n = 6$, the karyotype having a conspicuous long acrocentric chromosome pair with a large terminal satellite. White-flowered plants from near Kamieskroon, matching the type of the synonym, *M. diphylla*, have an identical karyotype. Plants from the type area of *M. diphylla* in the Clanwilliam district, also white-flowered, have either $n = 9$ or 5, the latter karyotype with one long metacentric and five acrocentric pairs. A similar karyotype occurs in plants with somewhat larger flowers from northern Namaqualand. A population from the Richtersveld at the extreme of the range of the subspecies has $n = 6$ and a comparable karyotype in which one very small metacentric chromosome pair stands out. There is probably more variation in the subspecies yet to be recorded, and it is premature to attempt to construct a hypothetical pattern of chromosome evolution for subsp. *filicaulis*. Available data suggest that $n = 9$ is the ancestral number.

Specimens examined. SOUTH AFRICA. CAPE: 29.17 (Springbok) Richtersveld, Eksteenfontein road 3–4 km N of the Port Nolloth–Steinkopf road (AB), *Goldblatt 5717* (MO, PRE); Spektakelberg (DA), *Barker 1340* (NBG), *7423* (NBG); near Okiep (DB), *H. Bolus 6616* (BOL); hills above Okiep, *Marloth 9880* (PRE); Springbok, *Esterhuysen 5879* (BOL); Blou Stasie, near Springbok, *Leighton 1173A* (BOL); sandy flats below Wildeperdehoek Pass (DC), *Goldblatt 5761* (MO); 21 km SW of Springbok (DD), *Acocks 19576* (K, PRE).

30.17 (Hondeklipbaai) granite hills 2 km N of Kamieskroon (BB), *Goldblatt 4254* (MO); Kamieskroon, *Lewis 5478* (NBG); 14 km NNW of Garies (BD), *Acocks 14964* (PRE); Buffels River to Soebatsfontein, *Leighton 1211* (BOL); Brakdam hills, *Schlechter 11111* (BOL).

30.18 (Kamiesberg) Kamiesberg, E slopes Rooiberg (AC), *Goldblatt 4308* (MO); sandy field below Studers Pass, *Goldblatt 635* (BOL); Kamiesberg between Roodeberg and Ezelskop, *Drège 2605* (K, MO, P); Koms Ravine (CA), *Pearson 6665* (K); between Bitterfontein and Garies (CA-CC), *Pillans 6346* (BOL), *Leipoldt 3846* (BOL).

31.18 (Vanrhynsdorp) 1 km N of farm Komkans, Kliphuis se Kop (AA), *Nordenstam & Lundgren 1710* (MO, NBG, S); 4 mi. N of farm Komkans, Geelkop, *Nordenstam & Lundgren 1720* (MO, S); Van Rhynsdorp (DA), *Barker 3642* (NBG); Vredendal Commonage, *Hall 3843* (NBG, PRE, STE); 10 km N of Van Rhynsdorp, *Acocks 19499* (M, NBG, PRE); N slopes of Gifberg (DC), *Goldblatt 207* (BOL); hills W of Trawal on the Kleipan road, *Goldblatt 5666* (MO).

32.18 (Clanwilliam) Lamberts Bay (AB), *Henrici 3300* (PRE); near Olifants River at Clanwilliam (BB), *Penther 734* (K); Ramskop, Clanwilliam, *Goldblatt 7376* (MO).

WITHOUT PRECISE LOCALITY: Richtersveld, *Marloth 12207* (BOL); Querung des Olifantsrivier, *Penther 554* (BOL); Namaqualand Minor, *Scully 111* (BOL).

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NOTES ON PERUVIAN PALMS[1]

ALWYN H. GENTRY[2]

ABSTRACT

Three new species of Peruvian palms are described: *Wettinia longipetala* A. Gentry, *Chamaedorea megaphylla* A. Gentry, and *Chamaedorea smithii* A. Gentry. In addition, the genus *Dictyocaryum* is reported from Peru for the first time, and new combinations are proposed for *Geonoma trigona* (Ruiz & Pavon) A. Gentry, *Chamaedorea poeppigiana* (Mart.) A. Gentry, and *Chamaedorea latisecta* (H. Moore) A. Gentry.

Palms are notorious for their taxonomic difficulty, due in large part to their size and consequent unwieldiness as herbarium specimens. Nevertheless, enough recent Peruvian palm collections have been generated by the re-activated Flora of Peru project (see Gentry, 1980) to begin to bring order out of their taxonomic near chaos. Each of the new species (plus two newly rediscovered species) described here is an important component of one of the specialized local vegetation types so characteristic of the interrupted system of parallel ridges that comprise the eastern slope of the central Peruvian Andes, yet none of them had been collected when Macbride (1960) wrote his "Flora of Peru" treatment. Since some of these vegetation types are highly endangered, the palms described here are of more than passing significance to conservation. That most of these species are among the commonest and most obvious plants in their particular type of forest emphasizes the inadequacy of floristic knowledge of the complex Amazonian/Andean interface in Peru, a lack that will soon be permanent if destruction of these habitats continues at current rates.

Dictyocaryum H. Wendl., Bonplandia 8: 106. 1860; ampl. Bot. Zeitung (Berlin) 21: 131. 1863.

Dictyocaryum lamarckianum (Mart.) H. Wendl., Bot. Zeitung (Berlin) 21: 131. 1863. *Iriartea lamarckiana* Mart., Hist. Nat. Palm. 3(7): 190. 1838. TYPE: Bolivia. Río Beni-Mamore watershed, *d'Orbigny s.n.* (not seen). Martius, Palm. Orbign. 18. t. 12: fig. 2. t. 20A. 1847.

Tree 10–25 m tall, 12–29 cm dbh, the trunk smooth, with faint leaf scars and no central swelling, the dense cone of stilt roots to 1 m tall, the crown shaft 1 m tall, green, abruptly swollen basally. Leaves 4–6, pinnately compound, 3–3.5 m long, with a petiole 50 cm long, the leaflets 26–35 per side, opposite to subopposite, each splitting fan-like into ca. 10 stiff laciniae held in different planes and conspicuously whitish below from a waxy coating. Inflorescence ca. 2 m long, erect in bud and at anthesis, in bud ca. 2 m long with 5 primary bracts and 3 bract scars, the 4 closed bracts rupturing with growth, the innermost subwoody and puberulous externally with rather flattened basally swollen trichomes, these largely caducous except the scale-like base, the inflorescence pyramidally paniculate, with ca. 45–50 erectly subhorizontal secondary axes, these mostly 3–4-branched ca. 7–15 cm from base, at maturity downcurving from the central axis from the weight of the fruit, near apex only staminate flowers, with pistillate flowers intermixed in triads with pairs of staminate flowers on basal 60%, the flowers white to yellowish, the male with 6 stamens. Fruit ovoid, 2–2.5 cm long when fresh, deep green.

Additional specimens examined. PERU. PASCO: Provincia Oxapampa, 20 km W of Oxapampa on road to Paucartambo, 1,970 m (75°28′W, 10°35′S), *Smith & Pretel 1655*; Oxapampa, 1,860 m (75°21′W, 10°34′S), *Smith & Brack 2941*; Oxapampa–Cerro de Pasco road, 20 km W of Oxapampa, 1,980–2,000 m, lower montane forest on steep slopes dominated by *Dictyocaryum*, ca. 10°45′S, 75°50′W, *Gentry, Smith, Vasquez & León 39921*. SAN MARTIN: Rioja Provincia, Campamento Garcia, km 384.5 Olmos–Moyobamba road, 2,250 m (77°21′W, 5°45′S), *Smith 4841* (all MO, USM, and to be distributed).

Although this is the first record of *Dictyocaryum* for Peru, the species described above is the absolute dominant in an interrupted band of montane forest that extends along much of the

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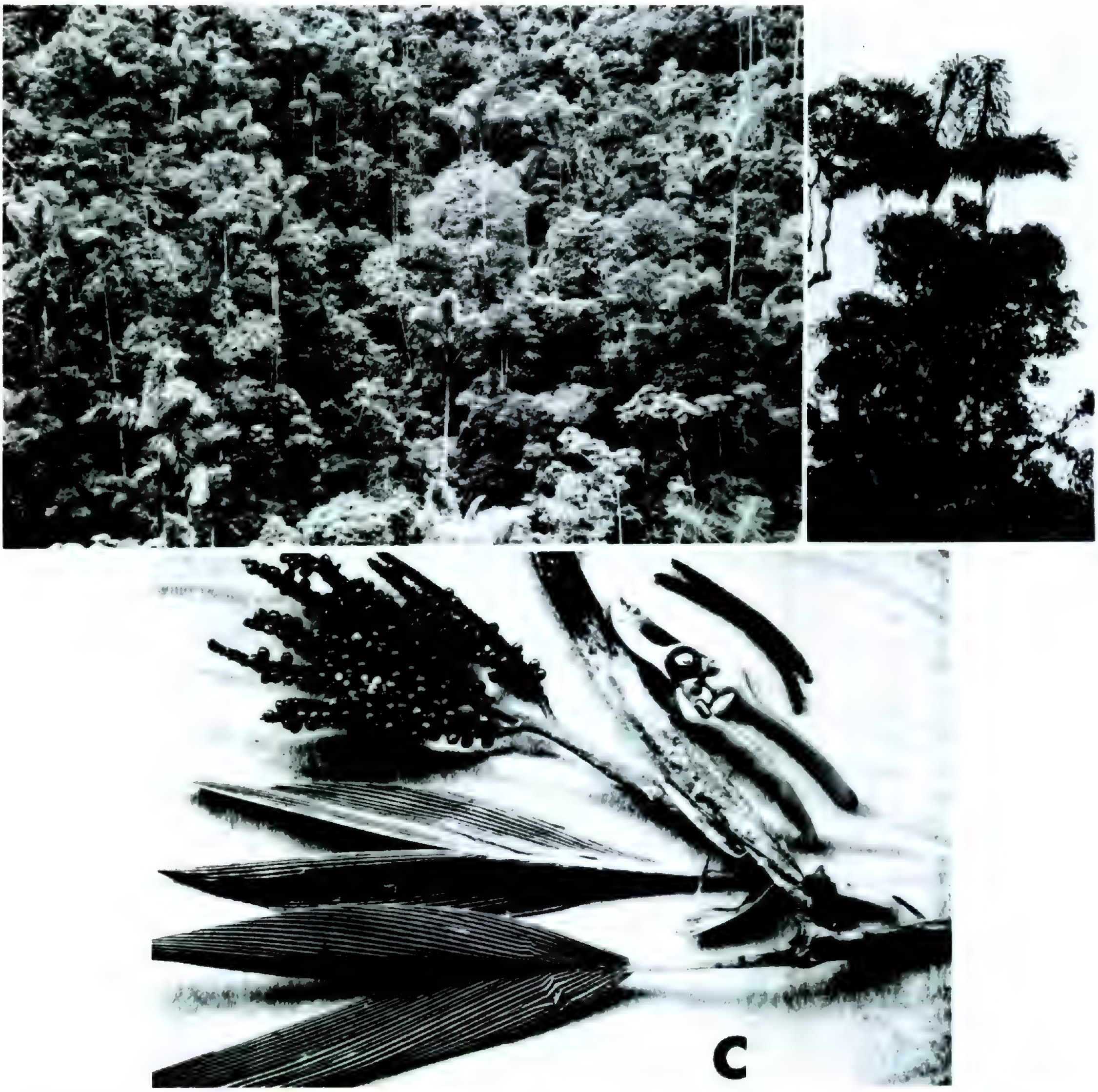

FIGURE 1. *Dictyocaryum* and *Geonoma*.—A. *D. lamarckianum* dominated forest at 1,900 m on Oxapampa-Cerro de Pasco road, 20 km W of Oxapampa; all palms in picture are *Dictyocaryum*.—B. Close view of pair of *D. lamarckianum* trees showing upright preanthesis inflorescence and suberect openly paniculate fruiting inflorescence.—C. *G. trigona*, fruiting inflorescence and leaves (the pruning shears are 22 cm long), *Gentry, Smith, Vasquez & León 40003* (MO).

eastern face of the Cordillera Oriental, mostly between 1,800 and 2,200 m altitude (Fig. 1A, B). It is known locally as "basanco" (Oxapampa) and "pona" (San Martin). In Burret's (1930) synopsis of *Dictyocaryum*, two Colombian species were recognized as well as one each from Bolivia and Venezuela. Subsequently two additional species of *Dictyocaryum* have been described, including *D. superbum* Bur. from southeastern Ecuador (Burret, 1940). The very incompletely described Ecuadorian species occurs at lower altitudes (1,200–1,400 m) and is thus unlikely, on phytogeographic grounds, to be conspecific with the Peruvian plant. Although identification of the Peruvian plant as conspecific with Bolivian *D. lamarckianum*, which also occurs at somewhat lower altitudes, is rather tentative, the Bolivian and Peruvian populations surely look the same in the field. In Bolivia, *Dictyocaryum* occurs mostly at somewhat lower altitudes [1,500–1,600 m; *Gentry & Solomon 44470* (MO) from La Paz Department, 4 km above Incahuara, 13.5 km above San Pedro, bosque pluvial subtropical sensu Holdridge, 67°35′W, 15°55′S]. Although

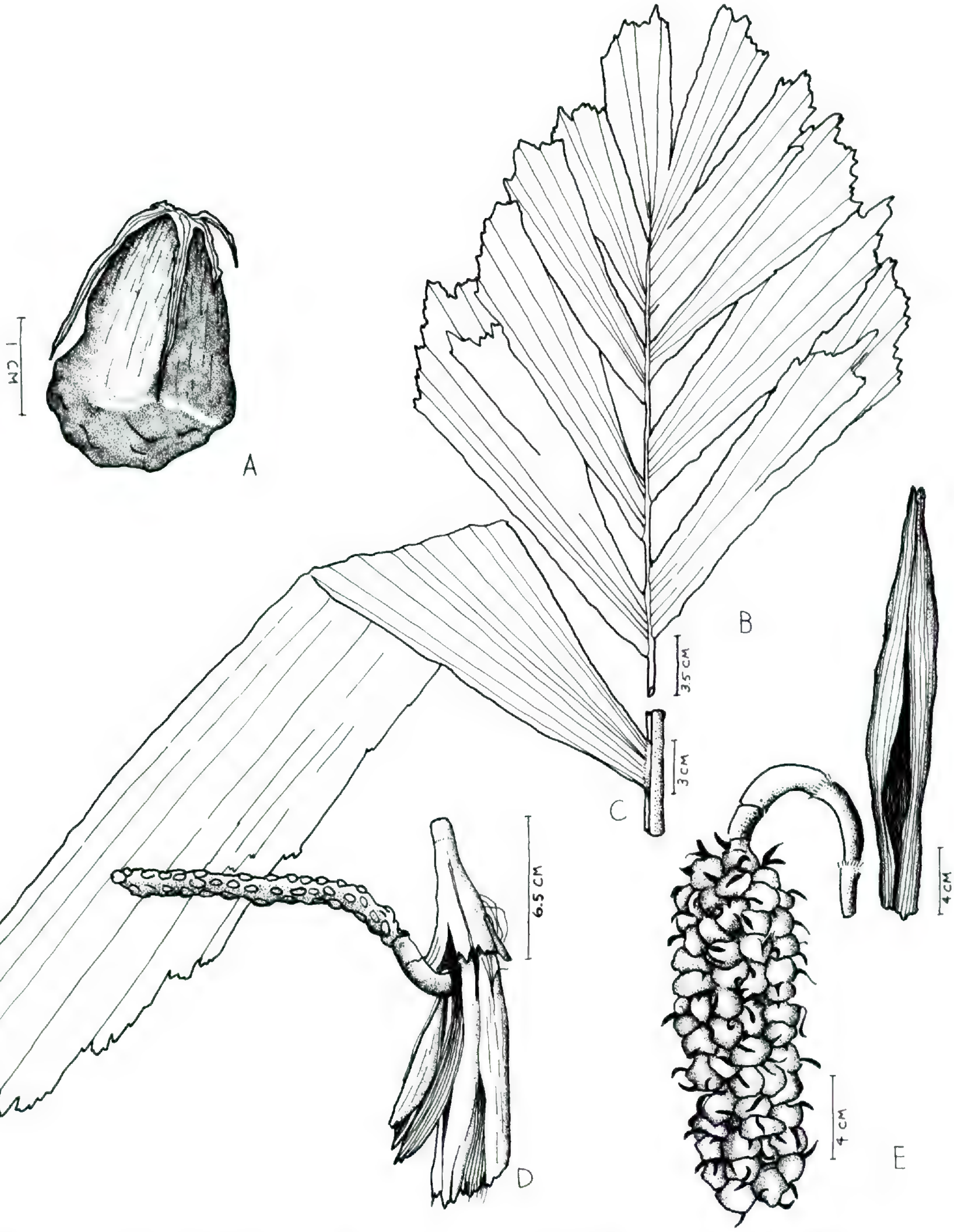

FIGURE 2. *Wettinia longipetala* A. Gentry.—A. Fruit.—B. Leaf apex.—C. Middle leaf segment.—D. Old infructescence with fruit fallen. A–D. *Gentry & Smith 36055* (MO).—E. Young infructescence and subtending bract, *Gentry, Smith & Jaramillo 42009* (MO).

less dominant than in Peru, the Bolivian plant also is an extremely conspicuous component of its habitat with eight individuals occurring in a 1,000 m^2 sample area near Incahuara, where it was the seventh commonest species.

Wettinia longipetala A. Gentry, sp. nov. TYPE: Peru. Pasco: Province Oxapampa, Serrania de San Matías W of Puerto Bermudez, near top of fila, 900–1,050 m, ridgetop thicket with lowland tree species, 10°25′S, 74°58′W, 15 June 1983, *Gentry, Smith & Jaramillo 42009* (holotype, MO; isotypes, MO, USM). Figure 2.

Caulis singulis. Pinnae foliorum indivisae. Inflorescentia non ramosa, floribus dense aggregatis, petalis florum femineorum (in fructu) 2–3 cm longis. Fructus trichomatibus curtis rigidis dense obtectus. Planta floribus femineis petalis longissimis a omnibus speciebus bene distincta.

Single-stemmed tree ca. 6 m tall with stilt roots at base. Leaves ca. 4 m long with ca. 30 leaflets on each side, the leaflets evenly arranged, undivided, subopposite at base, alternate at apex, to 50 cm long, broader (to 9 cm across) toward the asymmetrically praemorse apex, gradually and uniformly contracted to the 2–3 cm wide base, with numerous (mostly 10–12) uniformly thickened main veins, these tannish below, the surface puberulous below with numerous short, flat, suberect reddish trichomes, above with similar trichomes, but glabrescent, the rachis sharply angled above, rounded below, densely covered with flat appressed scale-like brownish trichomes, scabridulous. Inflorescences erect in bud, arising from an extended section of top of trunk, with ca. 4 bracts, the longest to 20–25 cm long, the outer bracts longitudinally striate, puberulous with appressed reddish trichomes, more or less glabrescent, the peduncle ca. 10–15 cm long, more or less rufescent with short erect trichomes, the single spike ca. 13–15 cm long, the petals of the female flowers (in fruit) longitudinally striate, linear, 2–3 cm long and 2–3 mm wide, exceeding the fruit, the sepals triangular, 5–7 mm long. Fruit densely appressed on the rachis, angular-obconical, densely scabridulous-rufescent with short reddish trichomes, ca. 2.5 cm long at maturity, subtended by the persistent tepals, the persistent linear style ca. 1 cm long.

This species is a distinctive and characteristic element of the ridgetop bamboo thickets of the Serrania de San Matías between the Ríos Pichis and Palcazu, a zone characterized as premontane rain forest under the Holdridge system. Further southwest, toward Villa Rica, it occurs at slightly lower altitudes (down to 700 m) on the steep slopes along the upper Palcazu tributaries.

Additional specimen examined. PERU. PASCO: drainage of Río Palcazu between km 51 and 60 of the new road in construction NW of Villa Rica toward Puerto Bermudez, 700 m, wet tropical forest in steep foothills, 10°30′S, 75°5′W, 4 Mar. 1982, *Gentry & Smith 36055* (MO).

This species is remarkable in the genus for the extremely long petals of its pistillate flowers, much longer than in any other species of the genus and at least twice as long as in any of the related single-spiked species. In Moore and Dransfield's (1978) treatment it keys out with *Wettinia augusta* Pavon & E. That species (as represented by four Peruvian collections, including topotypic material, at MO) differs, in addition to the much shorter petals, in having densely villous fruits. The short, rather scabrous, fruit indumentum of *W. longipetala* is highly unusual in subgenus *Wettinia* and more like that of some species of subgenus *Wettiniicarpus*. In Peru the two species are also ecologically separated, with *W. augusta* occurring at lower elevations (below 500 m) in tropical moist forest; the much commoner *W. maynensis* Spruce, which is very different in its branched inflorescences, occurs from the Amazonian lowlands to over 1,500 m, thus spanning the altitudinal range of both *W. longipetala* and *W. augusta*.

Geonoma trigona (Ruiz & Pavon) A. Gentry, comb. nov. *Carludovica trigona* Ruiz & Pavon, Syst. Veg. Fl. Peruv. Chil. 293. 1798. *Ludovia trigona* (Ruiz & Pavon) Pers., Syn. Pl. 2: 576. 1807. *Salmia trigona* (Ruiz & Pavon) Willd., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 5: 401. 1811. TYPE: Peru. Huanuco, *Pavon s.n.* [FI, not seen; MA (F negative 29563), destroyed fide Harling, 1958].

Treelet 2–3 m tall. Leaves bifid, thick-coriaceous, very closely plicate with ca. 20 ribs on each side, the blade ca. 30 cm long, 19 cm from apex to apex of midvein, the midvein ca. 12 cm long, the petiole ca. 15 cm long. Inflorescence once branched, the base of peduncle enclosed by a bract and the enlarged prophyll ca. 30 cm long, the tubular sheath thus formed subwoody, 2–3 cm wide, somewhat compressed, persistent, the peduncle 30–40 cm long, mostly enclosed by the prophyll and bract, the central axis well developed, the rachillae strongly ascending, 8–11 cm long, ca. 6–7 mm diam., densely brownish puberulous with mostly branched trichomes between the glabrate grayish lips, the flower pits with single conspicuous, bifid lower lip, spirally arranged in ca. 6 series, adjacent pits separated by 1 mm, the flowers (in bud) about 2 mm long, the stamen filaments linear, fused at base, ca. 1 mm long.

Additional specimens examined. PERU. PASCO: San Gutardo, Oxapampa–Cerro de Pasco road 30–35 km W of Oxapampa, elfin forest and "pajonal," 2,650–

2,800 m, 3 Feb. 1983, *Gentry, Smith, Vasquez & León 40003* (AMAZ, MO, USM).

The plant described above apparently represents the rediscovery two centuries later of a species previously known only from the type collected near Muña, Peru by Ruiz and Pavon and described by them in the wrong family. Rediscovery of this species thus resolves the long-standing mystery of the identity of *Carludovica trigona*.

Carludovica trigona, incompletely described, apparently from a sterile plant (though said to flower in April, May, and June), was for many years associated with the common Cyclanthaceae species now known as *Evodianthus funifer* subsp. *peruviana* Harling, and that species was treated as *Carludovica trigona* in the "Flora of Peru." The type material of *C. trigona* apparently was destroyed while on loan from Madrid to Berlin during World War II. In the process of preparing his monograph of Cyclanthaceae, Harling (1958: 273) examined a leaf from an isotype of *C. trigona* preserved at FI and realized that it belonged to Palmae rather than Cyclanthaceae. However, he did not propose the necessary new combination in *Geonoma*. No *Geonoma* similar to this species is included in the "Flora of Peru" (Macbride, 1960) or in Wessels-Boer's (1968) monograph of *Geonoma,* where it would key out with the very different pinnately compound-leaved Colombian species *G. dicranospadix* Burret. I originally intended to describe the recently collected plant described here as a new species. However, it seems clear from the type photograph that this distinctive palm, with its incredibly thick-coriaceous corrugate leaves, is, in fact, the same as *Carludovica trigona*.

Geonoma trigona turns out to be very characteristic in a very specialized shrubby xeromorphic high altitude vegetation locally called "pajonal." The distinctive "pajonal" vegetation type is characteristic of exposed ridges, mostly between 2,800 and 3,000 m, in the Cordillera Oriental of the Central Peruvian Andes. The "pajonal" interdigitates with "ceja de la montaña" elfin forest and is apparently edaphically limited, a conclusion supported by the extremely coriaceous leaf textures of many of its species. By far the most dramatically coriaceous "pajonal" species is *G. trigona* (Fig. 1C), which may have the thickest and most scleromorphic leaf of any palm in the world. The striking texture of the closely and rigidly plicate leaves of *G. trigona* suggests that it would be of great horticultural interest to palm fanciers, especially since its high altitude habitat indicates that it is probably cold resistant.

Chamaedorea poeppigiana (Mart.) A. Gentry, comb. nov. *Morenia poeppigiana* Mart., Hist. Nat. Palm. 3(7): 161. 1838; Hist. Nat. Palm. 3(9): 309. pl. 140, 141. 1849. *Nunnezharoa poeppigiana* (Mart.) O. Ktze., Revis. Gen. Pl. 2: 730. 1891. TYPE: Peru. Huánuco: Río Chinchao, *Poeppig 1546* [W, not seen (F negatives 29901, 29902)].

Morenia fragrans Ruiz & Pavon, Fl. Peruv. Prodr. 140. pl. 23. 1794; Syst. Veg. Fl. Peruv. Chil. 299. 1798. TYPE: Peru. Huánuco: Muña, *Ruiz & Pavon s.n.* [G, not seen (F negative 25383)], non *Chamaedorea fragrans* (Ruiz & Pavon) Mart., Hist. Nat. Palm. 2(1): 4. pl. 3: figs. 1, 2. 1823 (based on *Nunnezharia fragrans* Ruiz & Pavon). *Nunnezharoa morenia* O. Ktze., Revis. Gen. Pl. 2: 730. 1891 (nom. nov. for *Morenia fragrans* Ruiz & Pavon).

This relatively large *Chamaedorea* species with a 2–7 m tall trunk, is locally fairly common in wet premontane forest between 700 and 1,100 m on the eastern slopes of the Peruvian Andes. It is distinguished from other Peruvian species of the *Morenia* alliance of *Chamaedorea* by its narrowly lanceolate leaf segments. Recent collections have been made in San Martín, Huánuco, and Pasco departments, and Macbride (1960) cited earlier collections from Bolivia and from Amazonas Department, as well as the type from Muña. On the new Carretera Marginal in construction between Villa Rica and Puerto Bermudez, *C. poeppigiana* occurs in premontane rain forest on the same steep foothills of the upper Palcazu drainage as does *Wettinia longipetala.* [km 51–60, Villa Rica-Puerto Bermudez, 700 m, *Gentry & Smith 36000* (MO, USM)]. In San Martín Department it is known as "shucso negro."

I propose this new combination in anticipation of approval of Proposition 458 (Moore, 1979), which has already been unanimously approved by the Committee for Spermatophyta (Taxon 31: 541. 1982). Although *M. fragrans* is the type species of *Morenia* and the oldest basionym available for this plant, transfer of that specific epithet to *Chamaedorea* is precluded by the existence of *Chamaedorea fragrans* (Ruiz & Pavon) Mart., based on *Nunnezharia fragrans* Ruiz & Pavon. Apparently *Morenia poeppigiana* is

conspecific with *M. fragrans* as already suspected by Macbride (1960), and that specific epithet becomes the appropriate one for the species in *Chamaedorea.*

Chamaedorea latisecta (H. Moore) A. Gentry, comb. nov. *Morenia latisecta* H. Moore, Gentes Herb. 8: 203. 1949. TYPE: Colombia. Putumayo: Sibundoy, 2,225–2,300 m, *Schultes & Villareal 7676* (not seen, fide Moore, 1949, fig. 87).

The Peruvian *Chamaedorea poeppigiana* is not the only *Morenia* species for which a new combination is needed in *Chamaedorea.* However, of all the middle elevation species of *Morenia, M. latisecta* may be the only one adequately differentiated from *Chamaedorea montana* (Humb. & Bonpl.) Voss for specific recognition. It is distinguished by its broadly lanceolate leaf segments. If *Morenia* and *Chamaedorea* are merged under the latter name, the above combination is needed. I have refrained from proposing other new combinations in *Chamaedorea* in anticipation that several of approximately ten *Morenia* names apparently accepted by Moore (1979) will prove synonymous with *Chamaedorea montana* (Humb. & Bonpl.) Voss, which has the oldest available basionym and for which the combination in *Chamaedorea* has already been made.

Chamaedorea megaphylla A. Gentry, sp. nov. TYPE: Peru. Huánuco: Provincia Leoncio Prado, La Divisora, Cordillera Azul near border with Ucayali, 1,620–1,760 m, disturbed cloud forest, 75°48′W, 9°5′S, 10 Aug. 1980, *Gentry, Salazar & Horna 29572* (holotype, MO; isotypes, AMAZ, MO, USM).

Arbor dioeca, 5 m alta. Folia 2 m longa, pinnis utrinque plus quam 20, lineari-lanceolatis, pro parte maxima 50–58 cm longis. Inflorescentia feminea paniculata, ramis lateralibus 19–24. Flores feminei calycibus cupularis 2–2.5 mm longis, petalis ovatis, 3–4 mm longis.

Dioecious tree 5 m tall, the trunk ca. 4 cm diam., green, ringed. Leaves 2 m long, pinnate, the rachis triangular in section, acutely so toward apex, with over 20 pairs of opposite or subopposite segments, these averaging a pair every 10 cm except at apex (5 pairs in apical 22 cm), the segments linear-lanceolate, not noticeably sigmoid, 50–58 cm long for most of length, the terminal segments smaller and as little as 20 cm long, mostly 9–10 cm wide (the terminal segments as little as 3 cm wide), somewhat corrugated when fresh, drying gray-green with contrastingly tannish main veins below, mostly with ca. 10 main veins per segment, fewer in narrow apical leaflets, glabrous except for a few minute and very inconspicuous scales on underside. Inflorescence (only female seen) whitish in flower, turning green in fruit, the peduncle 34–36 cm long, semicircular in cross section and 2 cm across at base, bearing 5 chartaceous brownish bracts, these glabrous except for few minute scales, the lowermost attached at base, the second 2–3 cm above base, the third 9–14 cm above base, the fourth ca. 27–28 cm above base (and 8–9 cm below lowermost inflorescence branch), these bracts 3–4 cm wide when flattened, the uppermost bract much smaller and caducous (ca. 3 cm long), 3–4 cm below basal inflorescence branches, the rachis 15–18 cm long, with a well-developed straight central axis and ca. 19–24 lateral branches 9–18 cm long, the flowers not sunken into rachillae, adjacent flowers mostly separated by ca. 5 mm. Female flowers with the calyx lobes fused into a 2–2.5 mm long basal cupule, the ovate acute petals 3–4 mm long, sometimes with a more or less distinct dorsal keel, the thick triangular-patelliform ovary ca. 2 mm long and 3 mm across, the stigma lobes sessile at top of ovary, ca. 1 mm long, erect to horizontal.

This species is apparently endemic to the isolated cloud forest of the upper part of the Cordillera Azul between Tingo Maria and Aguaytia. This area, designated by the Holdridge system as premontane rain forest, is well known for its endemism [e.g., *Syngonium gentryi* Croat, and the frog *Dendrobates silverstonei* (Myers & Daly, 1979)]. The remnant patch of forest in which *C. megaphylla* was discovered has since been cut down and we searched in vain for additional material in 1982.

This species is quite unlike any taxon of *Chamaedorea* (or *Morenia,* which was erroneously differentiated as monoecious and with which it is more closely allied) treated in the "Flora of Peru" (Macbride, 1960) in its generally much larger dimensions. The only Peruvian species whose description approaches that of *C. megaphylla* is *Morenia macrocarpa* Bur., known only from the incompletely described type and a second topotypic collection from a lower altitude (600–700 m) in the Huallaga Valley. From its description, *Morenia macrocarpa,* of which I have seen no authentic material, differs strongly from

M. megaphylla in the linear leaf segments; Macbride (1960) suspected that *M. macrocarpa* might be synonymous with *M. linearis* (Ruiz & Pavon) Bur., which has similarly narrow leaf segments.

While it is clear that this species is new to Peru, it is more difficult to be sure that none of the many species of *Chamaedorea* (and *Morenia*) proposed from elsewhere in Latin America are not conspecific, since most descriptions are very incomplete. The only other species of *Chamaedorea* sensu lato known to me to have leaves as long as the 2 m ones of *C. megaphylla* is a collection from 2,000 m near Baeza, Ecuador [*Balslev & Madsen 10346* (MO)] that I have referred to "*Morenia*" *caudata* Burret, largely because that species was described from near its collection locality, but which is very different from *C. megaphylla* in its much narrower leaflets. Unfortunately leaf length of palms usually cannot be determined from herbarium material and very few of Burret's (1933, 1936) descriptions give leaf dimensions. More important, all of the described South American species of *Chamaedorea* (or *Morenia*) differ from *C. megaphylla* in having leaves with either many fewer segments or the segments much shorter and/or narrower and/or sigmoid, or the terminal segments broader and confluent. From the description, the only remotely similar species of *Chamaedorea* with median leaf segments as broad as those of *C. megaphylla* is *Morenia latisecta* H. Moore of Putumayo, Colombia (see above), but that species differs in shorter (0.3–1.3 m) leaves and the broadly lanceolate shape of its leaf segments.

I have not attempted to account for the plethora of Central American *Chamaedorea* names, but assume on phytogeographical grounds that none is relevant to the Peruvian species since it is quite unlike anything known from geographically intermediate Panama or Costa Rica.

Chamaedorea smithii A. Gentry, sp. nov. TYPE: Peru. Junín: Tarma-Chanchamayo border, Río Tulumayo drainage, Rondayacu, N of Monobamba, 45 km S of San Ramón, Podocarpus forest, 1,800 m (75°25′W, 11°20′S), 15 Oct. 1982, *Foster & Smith 9171* (holotype, MO; isotypes MO(3), USM, to be distributed).

Arbor parva, 2 m alta. Folia ca. 65–75 cm longa, pinnis utrinque 8–9, linearibus vel lanceolato-ellipticis, non sigmoidei, 15–29 cm longis, 1–5 cm latis. Inflorescentia feminea paniculata, pedunculo ca. 30 cm longo, rhachi recta, ramis lateralibus 15–21, fere perpendicularibus. Flores feminei calycibus cupularis 1.5 mm longis, petalis ovatis 1–1.5 mm longis. Fructus globosus, 0.8–1 cm diam.

Slender treelet 2 m tall, the stem green, with prominent rings. Leaves ca. 65–75 cm long, pinnate with 8–9 pairs of alternate or subopposite segments, adjacent segments mostly separated by 3–7 cm, the segments variable in shape, narrowly lanceolate-elliptic to linear, not sigmoid, 15–29 cm long, long acuminate, the lowermost less than 1 cm wide, some of the terminal and middle segments to 5 cm wide, drying grayish green with contrastingly tannish main veins below, mostly with 5–7 main veins, fewer in the narrow basal segments, the "main" veins intergrading into and not very strongly differentiated from the others, more or less minutely lepidote on underside of leaf segments, otherwise glabrous; petiole at least 9–15 cm long below lowermost segments. Inflorescence (only female seen) with peduncle ca. 30 cm long, bearing 4 narrow (ca. 1 mm wide) membranaceous bracts, the lowermost attached near base and ca. 8–9 cm long, the second attached ca. 4 cm above base and ca. 17 cm long, the third attached ca. 13–14 cm above base and ca. 31 cm long, the uppermost ca. 24–25 cm above base (7–9 cm below basal inflorescence branches) and ca. 5–6 cm long, the rachis 10–13 cm long, rather straight, the 15–21 lateral branches 3.5–5 cm long, nearly at right angles with rachis in flower, the flowers not at all sunken into rachillae (the scars actually slightly raised), adjacent flowers mostly separated by several mm. Female flowers with the calyx lobes fused into a cupule ca. 1.5 mm (to 2 mm when in fruit) long, the broadly obovate petals ca. 1–1.5 mm long, folded over bud, the thick triangular-ovoid ovary ca. 1.5 mm long, the 3 stigma lobes sessile at top of ovary, ca. 1 mm long, recurved. Infructescence with the lateral branches to 14 cm long, the fruits globose, turning red at maturity, 0.8–1 cm diam., subtended by the persistent and conspicuous calyx cup.

This species is apparently endemic to the lower montane *Podocarpus* forests of intermediate elevations in the central Peruvian Andes. Although *C. smithii* is locally very common in the remnant *Podocarpus* forest at Rondayacu, this is one of the last vestiges of this vegetation type in Peru. The new species must thus be regarded as a highly threatened one, helping emphasize the

need for an increased focus on conservation of the last remnants of this endangered vegetation type.

Chamaedorea smithii keys out in the "Flora of Peru" to the vicinity of *C. pauciflora* Mart. and *C. boliviensis* Damm. It differs from lowland *C. pauciflora* in non-sigmoid mostly broader leaf segments with more (5–7) main nerves, the branched inflorescence, and smaller (7–8 mm long and wide versus 10 mm long by 7–8 mm wide) fruits. From *C. boliviensis*, another Amazonian lowland species, it differs in much narrower (to 5 cm wide versus a described 7–7.5 cm wide) leaf segments, and the globose fruit. This species is also related to *C. lanceolata* Ruiz & Pavon, a widespread, common, and highly variable species, but differs conspicuously from that species (and its several potential segregates) in having a pyramidal inflorescence with a straight well-developed central rachis and short (less than 5 cm in flower), numerous (15–21) lateral branches.

While a few Central American species (e.g., *C. schippii* Burret of Belize and *C. sartorii* Liebm. of Mexico) have somewhat similar inflorescences, none of these has non-sigmoid leaf segments irregular in width and broad in part. Although I have not been able to check all the Central American species of the genus, no *Chamaedorea* species of southern Central America is at all similar to *C. smithii*, suggesting that it is phytogeographically highly improbable that it could prove conspecific with any of the poorly known Central American taxa not represented at MO.

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A GUIDE TO COLLECTING PALMS[1]

JOHN DRANSFIELD[2]

ABSTRACT

Because of their frequently bulky nature and unfamiliar morphology, palms need special attention if they are to be adequately collected. A guide is presented to indicate how to go about preparing good herbarium specimens of palms and what notes to make in the field.

The making of good herbarium specimens of palms is a laborious, time-consuming, and often rather unpleasant activity, and because of this many palm taxa are very poorly represented in herbaria. The general collector, faced with limited time and money and with the need to collect large numbers of plants to satisfy funding bodies or exchange agreements, tends to shy away from such awkward plants. To the specialist, however, the unhurried careful collection of a majestic palm can be immensely satisfying. It is probably too much to expect general collectors to use the amount of time spent by a specialist palm collector in the preparation of herbarium specimens, but with relatively little effort, the usual frustratingly inadequate palm specimen can be much improved. Guidelines for the collection of palms have already been provided by Tomlinson (1965) and, for climbing palms, Dransfield (1979). It is hoped that the present article will reach a wider audience and encourage more careful palm collecting.

ACCESS TO THE PALM

Low forest undergrowth and savannah shrub-like palms do not present many problems of access. Tall tree palms on the other hand can be very difficult to collect. There are three main methods of attack on such palms:

1. Tree climbers. In some parts of the tropics, local people are adept at climbing palms and when such people are employed as field assistants, the collecting of tall palms is usually relatively straightforward. However, some tree palms cannot be climbed because their trunk diameter may be too great, the trunks may be armed with spines, or the trunk and leaf bases may be infested with ants.

2. Climbing irons, loops, and ropes. Such mechanical aids to climbing are usually bulky and require courage and practice to develop skill in their use. In some parts of the world they may be the only means of getting at fresh material of leaves and flowers without felling the palm.

3. Felling. There is no doubt that the felling of a palm provides the best access for collecting. Where a palm is multiple-stemmed, the felling of one stem for collection will probably do little permanent damage. However, in single-stemmed taxa, the collector is faced with the dilemma of completely destroying the palm. Where such a palm is abundant, the sacrifice of one individual seems justified. Even when a palm is rare, it may be possible to find individuals that can be sacrificed with a relatively clear conscience to the collector, e.g., if the forest area is being felled in any case. If a palm is felled, maximum use should be made of the opportunity provided by making several good collections. In populated areas of the tropics, palms may be the property of local people even if the plants are obviously wild. Considerable tact may be required to gain permission for collecting. It is also important to be aware of the dangers involved in the felling of a large palm tree. Palm crowns often provide shelter for a whole range of animals such as ants, hornets, reptiles, spiders, scorpions, birds, and bats. Although the dangers are probably not too great, it is certainly advisable to work with care when cutting off palm sheaths and disturbing the leaves. It is also worthwhile to scan the crown with binoculars for hornets, wasps, and bees before felling is begun.

EQUIPMENT

The services of one or two knowledgeable local people make palm collecting much easier, more entertaining, and usually provide ethnobotanical data. A "parang" or machete and a good pair of

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[1] I am grateful to Carol Buckman for preparing the plates.

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secateurs are essential equipment. Secateurs should be of the type with two cutting edges rather than the type with a single blade working against a flat surface, favored by some collectors. Strong rough leather gloves are invaluable; it is best not to use gloves consisting of leather palms and canvas backs as these give insufficient protection to the backs of the hands. An axe may be invaluable but of course is yet one more heavy item to carry. A large supply of hanging tags with long strong thread is essential. The quality of collections is greatly enhanced by copious field notes, therefore a collecting book with plenty of room for notes is also essential. Photographs are of great value; the collector may wish to include a supplementary wide-angled lens with the photographic equipment, as it is frequently very difficult to photograph entire tree palms within forest with only a standard or macro lens. A supply of formalin acetic alcohol (F.A.A.) in wide-mouth plastic bottles and some muslin are important items for the preservation of material for morphological or anatomical study.

The method of preservation of the herbarium material will vary with local circumstances. It must be said, however, that in humid tropical conditions the modified Schweinfurth method using newspapers, methylated spirits or industrial alcohol, and large, thick gauge polythene bags is the easiest way of dealing quickly with the day's palm collections. Even during the dry season in savannah areas, it may take an inordinately long time to dry bulky palm material in the sun or over plant driers, and the longer drying takes, the more the flowers and fruits are likely to become detached from inflorescences and infructescences.

What to Collect

It is not proposed to discuss palm morphology in great detail in this guide, although a certain amount of discussion will be necessary for an understanding of what organs need to be collected. Those interested in a more detailed morphological account should refer to Moore (1973) and Moore and Uhl (1982).

For some genera sterile collections are useless, whereas for others, especially the Asiatic climbing palms, they can be of considerable value. Variation in leaf dissection is a feature of several undergrowth genera such as *Pinanga, Iguanura,* and *Geonoma,* and in these genera supplementary sterile collections illustrating leaf variation are useful although not as reliable as when inflorescences can be collected too. Dead inflorescences and infructescences are well worth collecting if no fresh material is available or if fresh material is only sufficient for a unicate or one duplicate. When the frustrating circumstances arise of not being able to climb or fell a tree, fallen leaves and inflorescences, accompanied by photographs and good notes, will make a relatively good collection.

Deciding what parts of the palms should be collected is really a matter of common sense—how can the morphology of the whole palm be represented in the herbarium. A good collection should comprise adequate samples of all the organs of the palm available, coupled with notes to allow a reconstruction of the habit, dimensions, color, "hang" of leaves and leaflets, odor of flowers and fruit, and should be accompanied by ecological and ethnobotanical data (see Fig. 7). Ripe seed may be collected at the same time and be grown for research or ornamental purposes (see below), and pollen samples also can be conveniently made directly in the field.

In making collections, it is advisable to cut all palm pieces to the approximate size of a folded sheet of newspaper. It may not be possible or desirable in some instances (e.g., prophylls or peduncular bracts) to cut the object at all, and such larger objects may always be treated separately, however, it does help considerably if fragments are more or less of the same size. Each fragment must carry a hanging tag bearing the collection number written in pencil or ink insoluble in water or alcohol. This cannot be stressed too strongly; however, it does mean that a large supply of tags is essential. In building up a bundle to be treated with spirit using the Schweinfurth technique, experience has shown that the most satisfactory method is to begin by laying down four double thicknesses of newspaper opened out (Fig. 1a). This becomes the wrapping of the finished bundle (Fig. 1b). It is best to begin with flat leaf fragments, placing them in double or single folds of newspaper, and progress inwards to spiny or bulky fragments in the middle (to prevent puncturing of the polythene bags), followed by less bulky, flatter material at the top. The bundle can then be tied up within the four folds of double thicknesses of newspaper (Fig. 1b). The bundle is then put into a polythene bag, doused with spirit (it may be necessary to make holes in the top end of the newspaper folds to allow spirit to get to the mid-

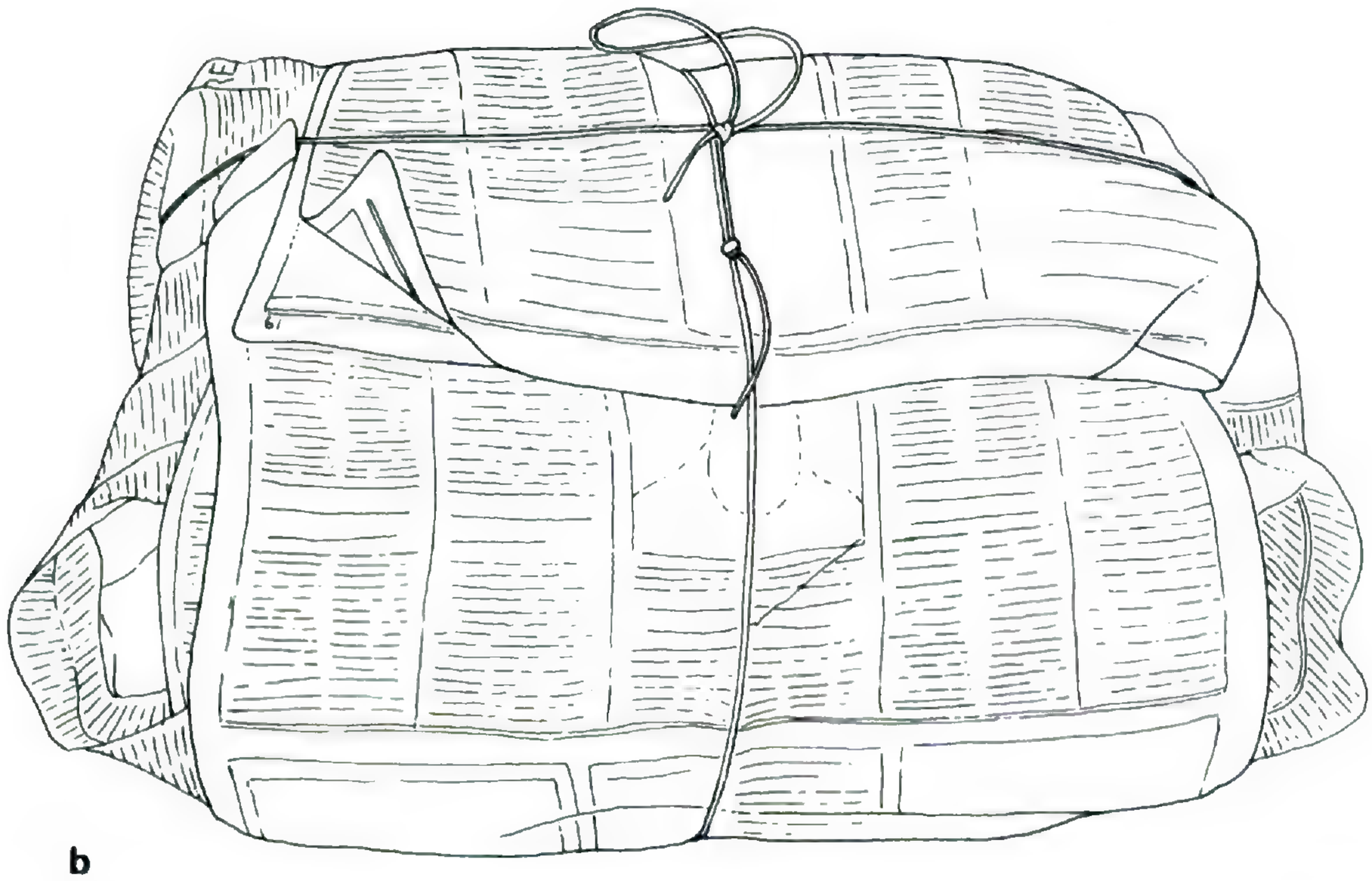


FIGURE 1.—a. Starting a bundle of palm specimens.—b. A finished bundle for enclosing in plastic and dousing with spirits.

dle of the bundle), and then tied up; the whole can then be put into a second polythene bag for safety. Because of their bulkiness it has been found that many palms, if well pressed and packaged, can put up with a certain degree of rough handling if the polythene covered bundles are sewn up in hessian sacks. They can tolerate two to five months in transit if well soaked with spirit (before shipment it is advisable to check the state of the bundles in case drying out has occurred).

In the following notes, the general morphology of palms is briefly discussed, the parts necessary for a good collection indicated, and the need for notes explained.

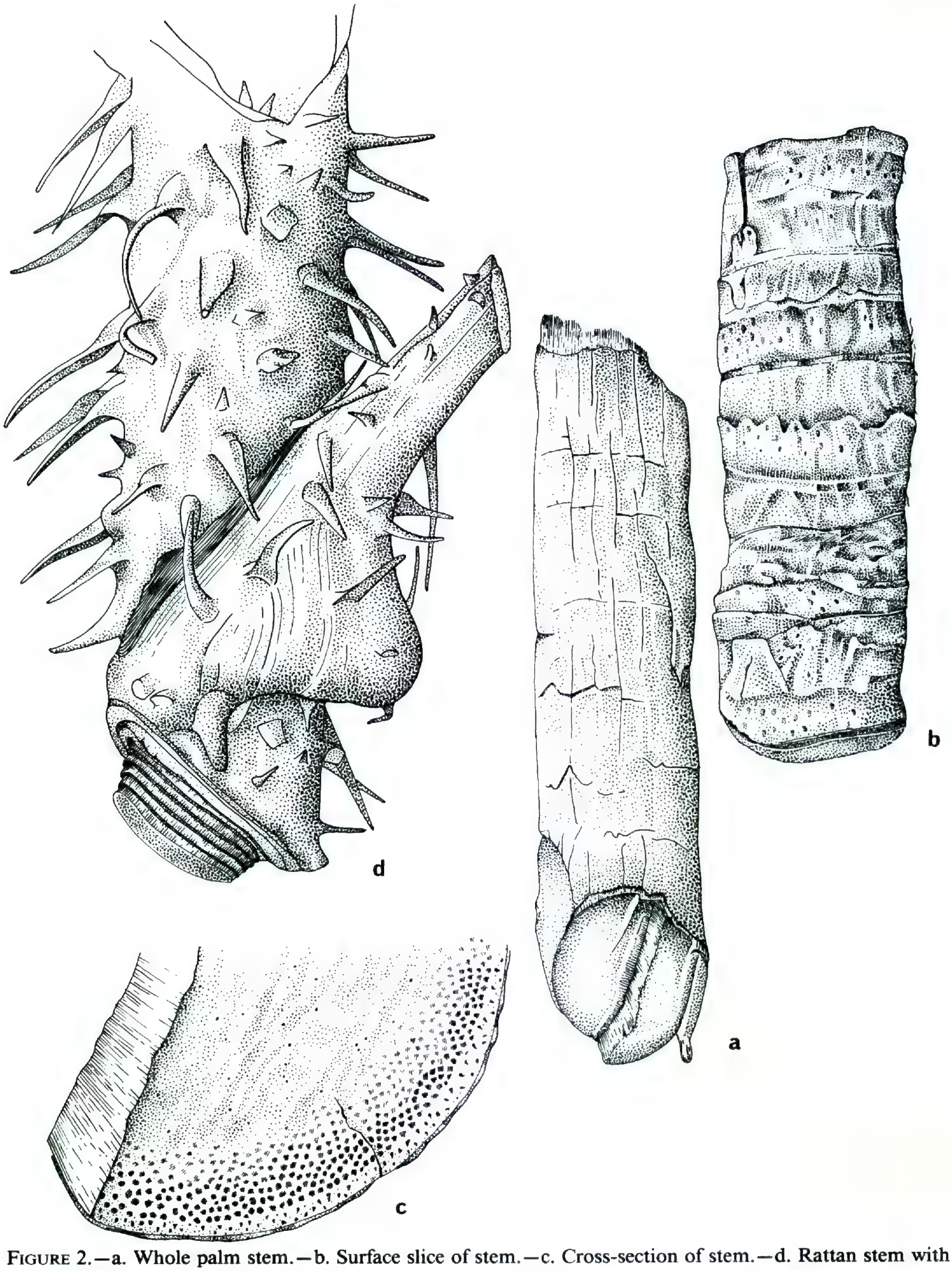


FIGURE 2.—a. Whole palm stem.—b. Surface slice of stem.—c. Cross-section of stem.—d. Rattan stem with leaf sheaths.

WHAT TO NOTE AND WHAT FRAGMENTS TO TAKE

General data. Locality, habitat, elevation, vernacular name and uses, and date.

Habit. Note whether palm is single-stemmed or clustered; if clustered whether the clump is close or diffuse, whether with stolons or not. Note whether the palm is a tall tree, or undergrowth palm, or "stemless" or climbing, whether stilt-

rooted or not. Estimate the total height. Photographs showing habit are of great value.

Stem. Note whether stem is bare or obscured with leaf sheaths or bases, whether aerially branched or not; if the stem is bellied this should be noted; note any armature, the type of nodal scars and the color. Measure the diameter with and without leaf sheaths, and the length of the internodes; estimate the total length if different from the palm height.

In small palms, collect a length of stem (Fig. 2a), which can be split vertically if necessary (Fig. 2b), and in large palms take a sample of the outer stem as if for a regular bark sample (Fig. 2c).

Roots. Note any peculiar rooting behavior (e.g., stilt-roots, spine-like adventitious roots, apogeotrophic breathing roots, etc.). Collect samples or roots where appropriate.

Leaf in general. Note number of leaves in crown, their arrangement (distichous, tristichous, or spiral), whether neatly abscissing, marcescent, or persistent, and try to describe general "hang" of leaves. Photographs showing leaf hang are invaluable.

Leaf sheath. Note whether tubular (Fig. 5c) or open (Fig. 5d), position of any splits, whether forming a crownshaft (Fig. 5c) or not, whether becoming fibrous; note any armature, indument and color. Measure length and width or diameter.

Collect whole sheath when small (Fig. 3a), and where large, collect sections of the sheath to include the base and apex, especially the junction of the sheath with the petiole. In climbing palms it is convenient to take the sheath sample as a section of stem and its surrounding sheaths that need not be removed (Fig. 2d).

Petiole. Note presence or absence; if present note any general features of indument and armature. Measure length and, where too large to represent, width.

If short, collect whole petiole including the insertion of the first leaflet or base of the lamina (in fan palms). If long, collect portions to illustrate any changes in form or armature along the length and a piece to include the insertion of the first leaflet or base of the lamina (Figs. 2a, 3c).

Blade. Note general characteristics and dimensions; whether palmate, costapalmate, pinnate, bipinnate, entire, or bifid. Measure the length of the rachis or costa.

In pinnate palms note the number of leaflets on each side and how they are arranged (regularly, grouped, in one plane or several, pendulous, etc.) and any special color features.

In palmate palms note the number of segments where leaf too large to collect whole, whether stiff or pendulous, and any special color feature.

Collect whole leaf where very small; the blade may be folded up if necessary. When of moderate size collect the base of the blade (Fig. 3a), a mid-portion (Fig. 3b), and the leaf tip (Fig. 3c), the leaflets or segments may be removed from one side of the rachis. When very large, the same samples are required but they may comprise one or two leaflets only; the rachis may have to be split and the leaflets folded up. In fan palms collect the tip of the petiole with the blade base (Fig. 4c) and hastulae and basal segments on one side, and two pieces of blade to include the central segments and lateral segments (Fig. 4d).

In climbing palms. In addition to the above features, note the position of the climbing whips—whether an extension of the leaf rachis (cirrus) (Fig. 5a) or borne on a leaf sheath (sterile inflorescence = flagellum) (Fig. 5b). Collect a sample climbing organ, which may be folded up (use gloves!).

Inflorescence. Note position—suprafoliar, interfoliar, or infrafoliar, whether solitary or multiple, and whether shorter or longer than the leaves. A photograph of the whole inflorescence would be very helpful. Note the sex (if possible), whether hermaphrodite, polygamous, monoecious, staminate, or pistillate (in dioecious species never ever mix sexes in the same collection number; give them each a separate number).

Peduncle. Note orientation and measure length; note any special features of indument.

Primary bracts. Note number; the prophyll (Bract 1) is often obscured by leaf sheaths but is of considerable taxonomic importance.

Rachis. Note length.

Branching. Note whether inflorescence branched or unbranched and count the numbers of orders of branching. Where first order branches are distant and highly differentiated, so-called partial inflorescences can be distinguished; when so, their number should be recorded.

Rachillae. Note length, orientation, and color.

Flowers. Note color and scent. Close-up photographs of flowers are very useful. Even fallen flowers may be of value.

Collect. If small, collect the whole inflorescence (thus saving much of the above note-taking), taking great care not to miss the prophyll. The prophyll may be caducous; if so it should be searched for on the ground or among the leaf sheaths. If large, then collect the pro-

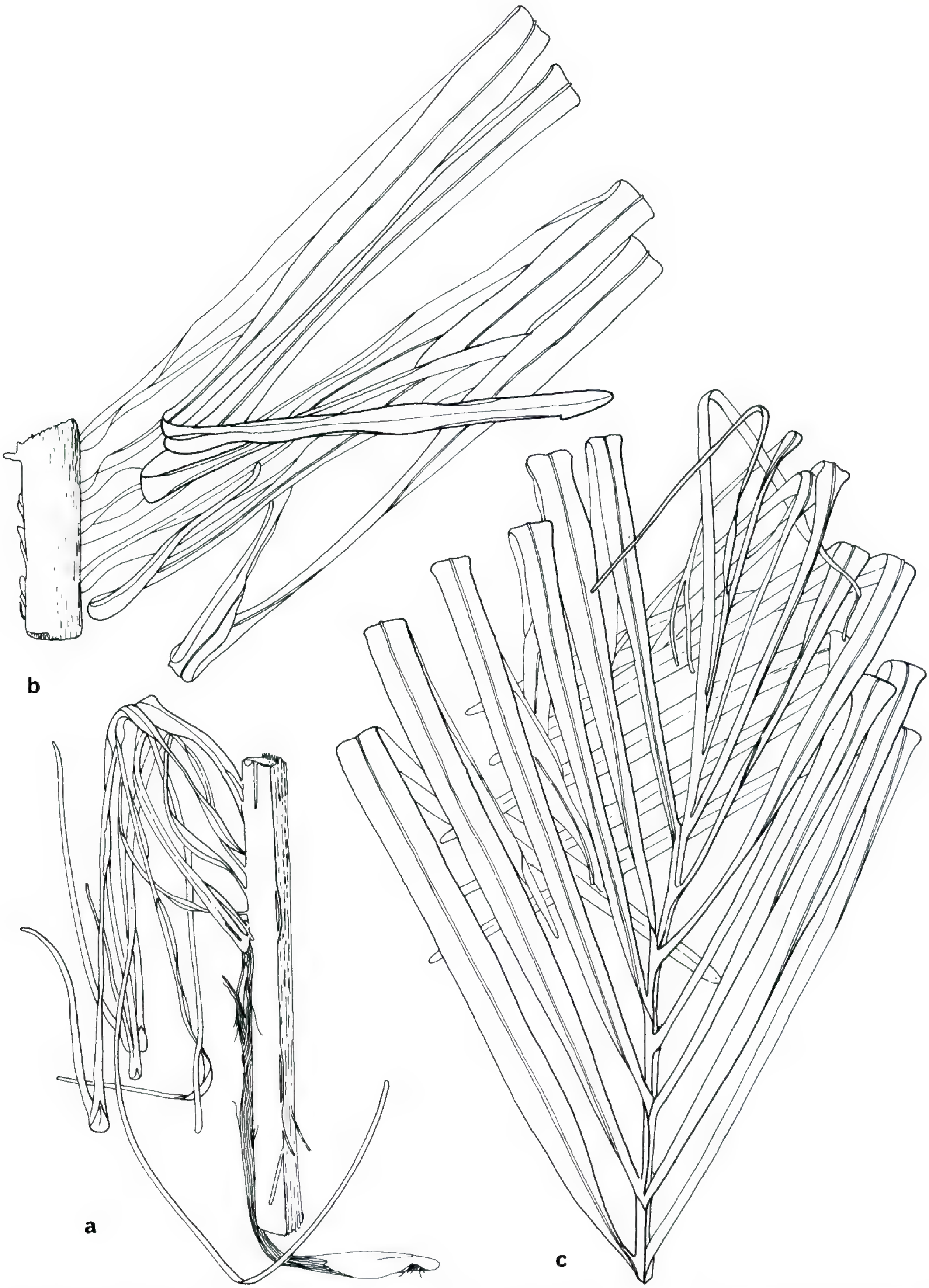


FIGURE 3. Pinnate leaf prepared for pressing.—a. Base.—b. Middle section, pinnae of one side removed.—c. Tip.

phyll and representative primary bracts, a portion of the peduncle, rachis (Fig. 6), and rachillae.

Try to collect more than one stage of development from the same palm; if not possible, do not mix numbers. Inflorescences from the same palm may be cut up later so that each duplicate has a major inflorescence represen-

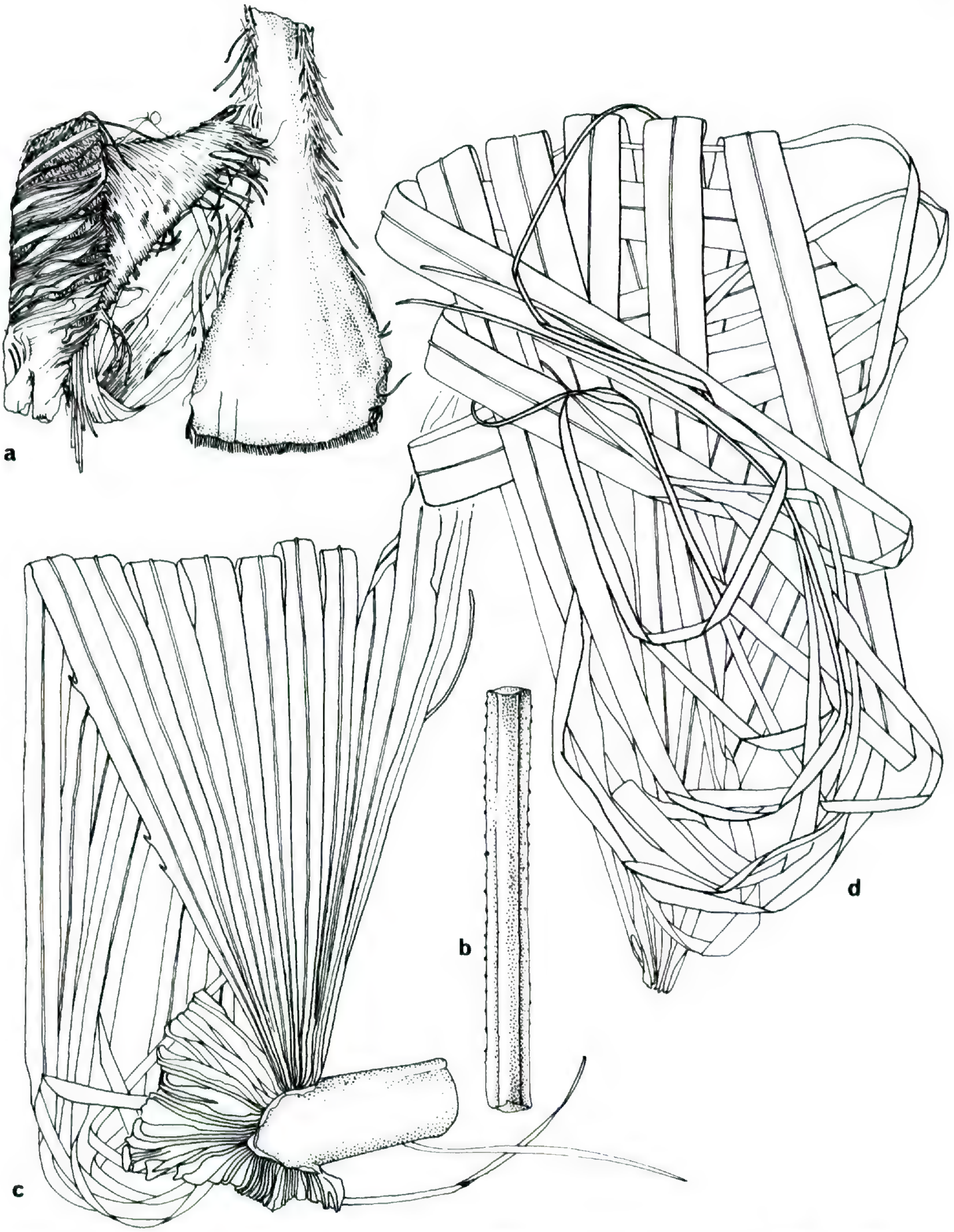


FIGURE 4. Palmate leaf prepared for pressing.—a. Sheath.—b. Petiole section.—c. Base of blade with all segments removed except at one side.—d. Middle portion of blade.

tation coupled with fragments (rachillae) at different stages.

Fruit. Note any color difference between inflorescence and infructescence. Note color of fruit. Close-up photographs of fruit are helpful. Collect infructescence, rachillae, and fruit.

Seedlings. Seedlings at the foot of a palm may not belong. They should be included with the main collection only when there is no doubt as to their provenance.

PALM SEED

Ripe palm seed is easily transported without loss of viability if germination requirements are understood, and the opportunity to collect seed

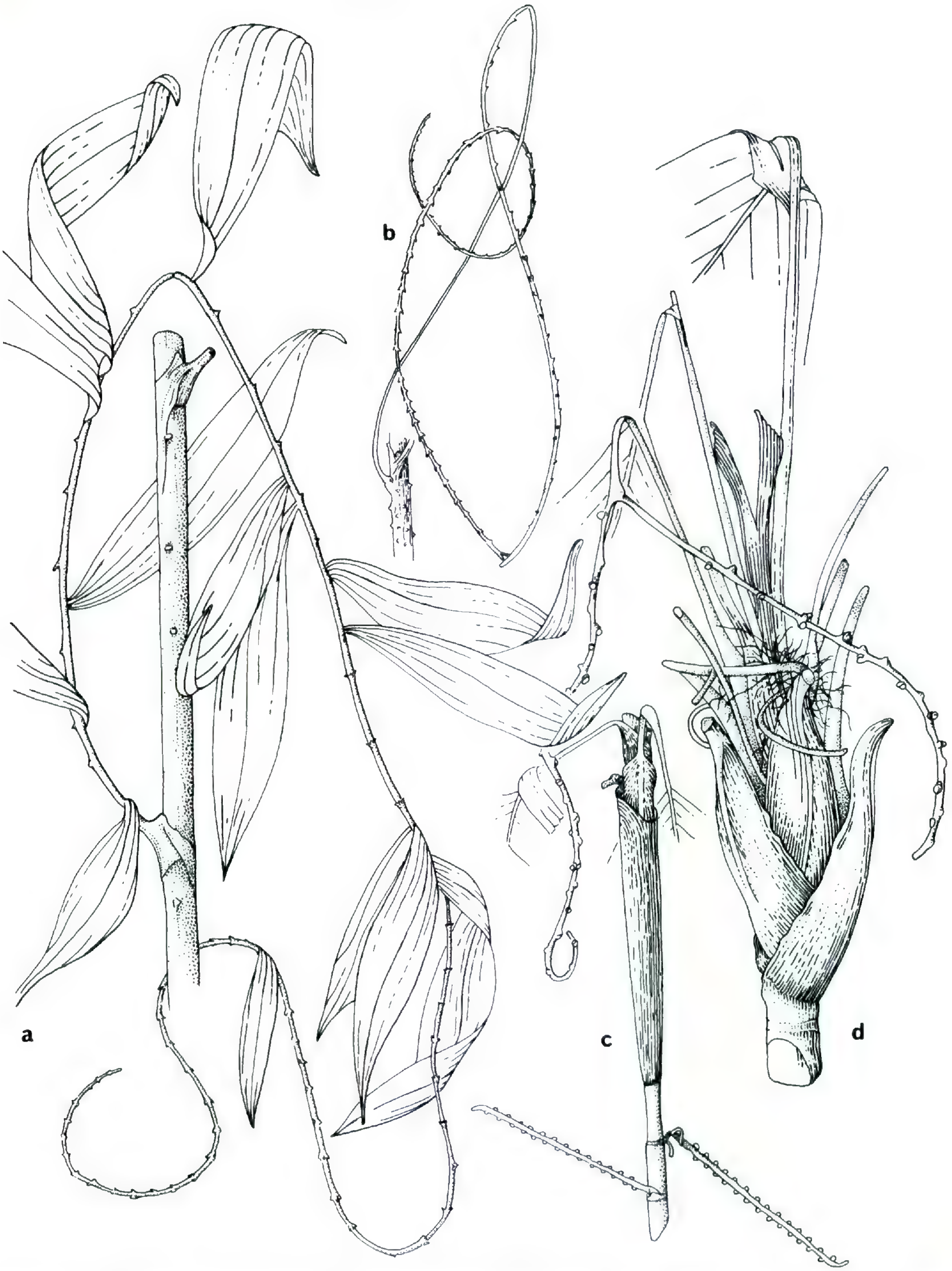


FIGURE 5.—a. Rattan with a cirrus.—b. Rattan with a flagellum.—c. Stem bearing a crownshaft.—d. Stem bearing open sheaths.

should not be wasted. There is a great demand for palm seed for ornamental purposes, both from botanic gardens and amateur enthusiasts. Furthermore, it is sometimes possible, though tricky, to obtain chromosome counts from the root-tips of seedling palms, and the seedling stages of many species are not known and could be usefully recorded by growing seed of known source. The

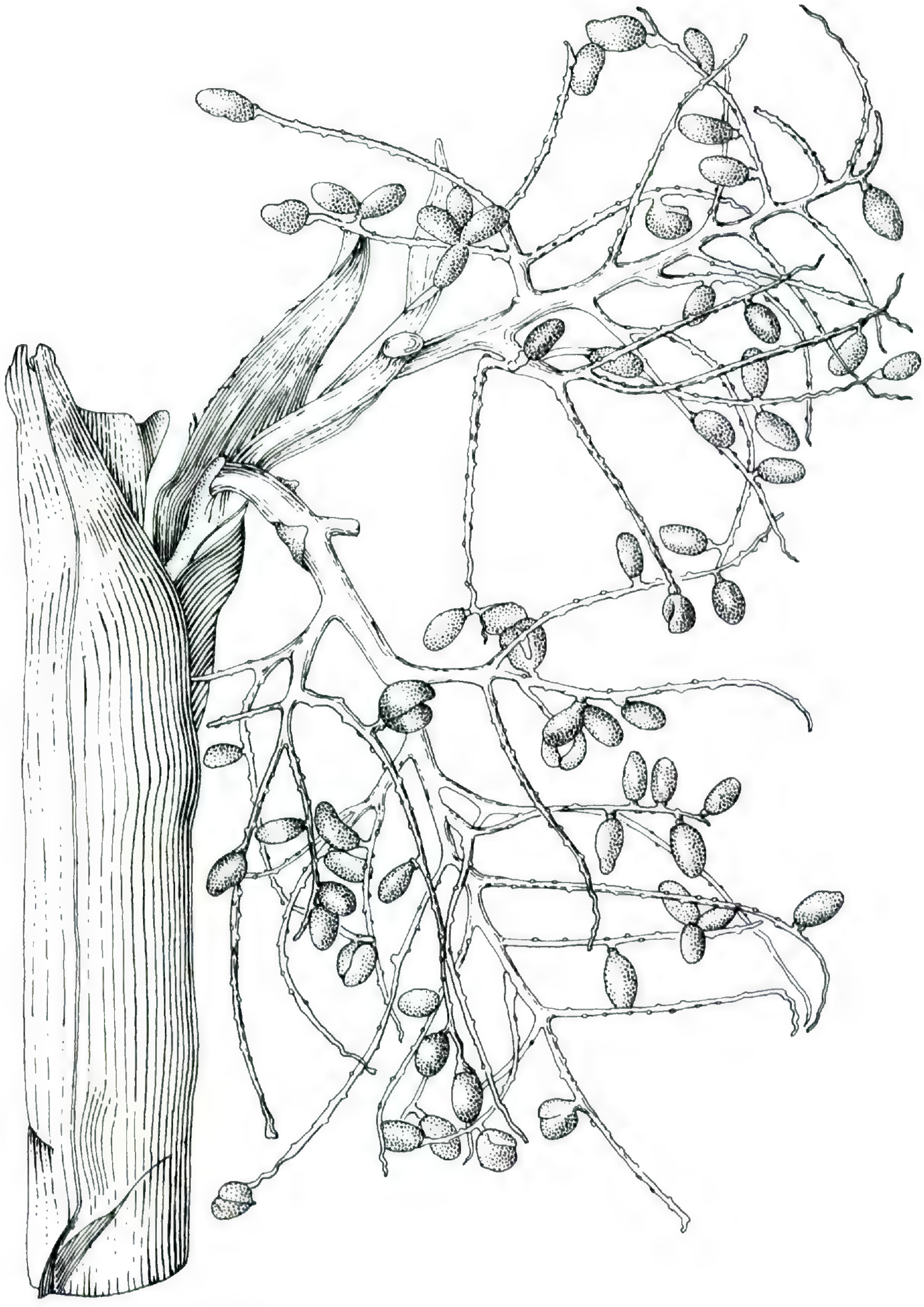
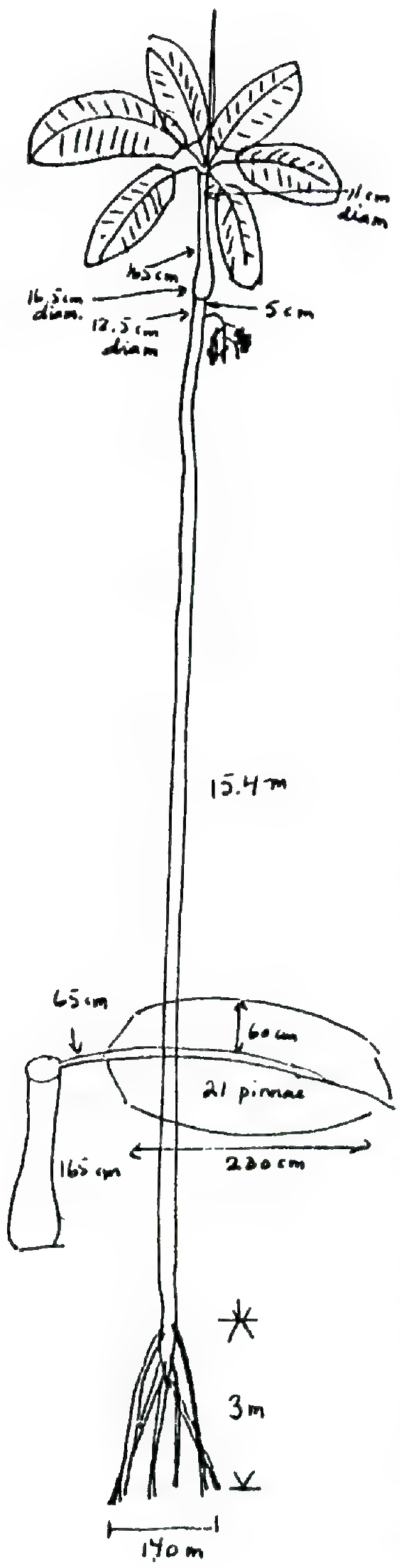


FIGURE 6. Portion of an infructescence.

International Palm Society's Seed Bank acts as a distribution center for palm seed, sending seed to botanic gardens and its members. Collectors contemplating gathering seed should be aware of phytosanitary and conservation regulations and may also wish to consult the Seed Bank. Ripe seed should be cleaned of any soft pulp. This is often most easily effected by trampling on the whole fruit in a bag and then allowing the pulp to rot for a couple of days; the seed may then be easily cleaned in water. Seed should then be packed damp (not wet) in sphagnum or soft toilet tissue in polythene bags and then posted airmail or carried. Seed may happily germinate in the bags and may be stored for several months. Drying out is lethal to most palm seed.



HERBARIUM KEWENSE
PALMAE

ARECACEAE
Socratea sp.

Spanish: "Chonta cade"

ECUADOR, Prov. PASTAZA: 4 km south of Shell towards Madre Tierra, just west of Puyo (01°30'S; 78°03'W). Remnants of tropical forest, 1050 m elev. 16 Mar 1983.

A soliatry tree in remnants of virgin forest, but often left in otherwise deforested areas. The base of the trunk is lifted from the ground by about 15 up to 3 m long and 5-8 cm in diam, brown, spiny adventitious roots that form a loose open inverted cone, 3 m high and 140 cm wide at the base. Trunk straight, smooth, grey, 15.4 m long, abouth 13 cm in diameter throughout. Crown of 6 expanded leaves and 1 lance-like, erect young leaf in the center; crownshaft 165 cm long, 16.5 cm in diameter at the base, tapering to 11 cm apically; petioles 65 cm long; blades 230 x 120 cm with 21 pinnae on each side, each pinna divided and the base twisted on the rachis so it forms a fan in a plane perpendicular to the rachis and the entire blade is therefore 3-dimensional, almost with the appearence of a fox's tail. Inflorescence inserted 5 cm below the crownshaft, the peduncle first ascending, then dropping into the rachis which bears long hanging branches of 1st order only. Fruits immature, green. Uses: According to Sr. Armando Ortiz Silva, lumberman, carpenter and agriculturer in Moravia, the fruit is not eaten, the trunk is soft and not good for construction purposes. The palmhart is sometimes good, but this one prooved bitter, maybe because the crown had a young lance-like leaf in the middle. According to the maid at hotel Turingia in Puyo, however, the seeds are eaten when young and soft.

Duplicates: QCA, Latinrecu, NY, K, AAU.

H. BALSLEV & L. BRAKO No. 4279

Socratea rostrata Burret
(vel valde aff.)
DET. J.DRANSFIELD 24.6.1983

FIGURE 7. An exemplary herbarium label.

MATERIAL FOR LIQUID PRESERVATION

Material preserved in formalin acetic alcohol (F.A.A.) is ideal for most morphological and anatomical studies and for illustrations of flowers. F.A.A. is made by mixing 90 parts of 50% ethyl alcohol, five parts glacial acetic acid, and five parts concentrated formalin. After fixation in F.A.A. for a few days material can remain in F.A.A. or be transferred to 70% ethyl alcohol,

allowing the F.A.A. to be used again. F.A.A. can only stand a little re-use, but it is useful to know this where space and resources are limited. Wide-mouth bottles are essential. Fragments for preservation should be clearly labelled with a tag written in pencil and then should be wrapped in a piece of muslin or gauze and placed in F.A.A. in a bottle. The use of muslin allows for the inclusion of several different collections in the same bottle and also helps decrease damage during inevitable shaking. The most useful fragments for preservation are samples of rachillae with flowers at various stages of development and fruits at various stages of maturity. If inflorescence primordia are available (search among the young leaf sheaths) these can be of great value and should be preserved entire, where possible. In more specialist collecting, samples of stem, root, petiole, rachis, and lamina should also be included with the reproductive organs in the liquid preserved collections.

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CATALOG OF THE MOSSES OF CHINA[1]

PAUL L. REDFEARN, JR.[2] AND P.-C. WU[3]

This catalog lists in alphabetical order 2,264 taxa (2,004 species, 21 subspecies, 196 varieties, and 20 forms) in 409 genera and 688 synonyms of mosses reported in the literature for China (including Taiwan). The major sources of the taxa included in this list are "Genera Muscorum Sinicorum" (Chen et al., 1963, 1978), "Index Bryoflorae Formosensis" (Lai & Wang-Yang, 1976), and "A Glossary of Terms and Names of Bryophytes" (Wu, 1984). Additional taxa, particularly for mainland China, are reported in the publications by Müller (1896, 1897, 1898), Brotherus (1924–1925, 1929), Thériot (1932), Dixon (1933), Bartram (1935), Varde (1937), Tixier (1966), Gangulee (1969, 1971, 1972, 1974, 1976, 1977, 1978, 1980), Liao-ning Provincial Agriculture and Soil Research Institute (1977), X.-j. Li et al. (1985), Gao & Chang (1983), Koponen et al. (1983), Iwatsuki & Mizutani (1983), S.-h. Lin (1984), Wu (1982), and Wu et al. (1986). A number of other publications were useful in preparing this catalog. Listed by family, these papers are: Archidaceae (Snider, 1975), Bartramiaceae (Ochi, 1962, 1963), Brachytheciaceae (Robinson, 1962; Takaki, 1955a, 1955b, 1956; Ochyra, 1982), Bryaceae (Mohamed, 1979; Koponen et al., 1982b), Calymperaceae (P.-j. Lin, 1984), Diphysciaceae (Iwatsuki, 1976b), Dicranaceae (Noguchi, 1968a; S.-h. Lin, 1981; Tan & Koponen, 1983), Ditrichaceae (Frisvoll, 1985), Encalyptaceae (Horton, 1982), Entodontaceae (Buck, 1980; Hu, 1983; Inoue, 1983), Fabroniaceae (Buck & Crum, 1978; Taoda, 1977a, 1977b), Fissidentaceae (Iwatsuki, 1980; Iwatsuki & Suzuki, 1982; Z.-h. Li, 1984), Grimmiaceae (Bremer, 1980a, 1980b, 1981), Hylocomiaceae (Koponen, 1979), Hypnaceae (Ando, 1956, 1957, 1958, 1963, 1964, 1965, 1966, 1969, 1972, 1973a, 1973b, 1976, 1978; Iwatsuki, 1965), Leskeaceae (Iwatsuki, 1976a), Leucobryaceae (Iwatsuki, 1977b), Leucodontaceae (Zhang, 1982), Mniaceae (Koponen, 1971b, 1972, 1981; Koponen & Lai, 1978; Koponen & Lou, 1982), Meteoriaceae (Noguchi, 1976), Myuriaceae (Iwatsuki, 1979), Neckeraceae (Ninh, 1984; Noguchi, 1984), Orthotrichaceae (Vitt, 1972, 1980a, 1980b), Plagiotheciaceae (Iwatsuki, 1970; Ochyra, 1976), Polytrichaceae (Xu & Xiong, 1982; Nyholm, 1971), Pottiaceae (Chen, 1940, 1941; Saito, 1972, 1975; Sollman, 1983; Zander 1978, 1979), Pterobryaceae (Miller & Manuel, 1982), Ptychomitriaceae (Noguchi, 1968b), Rhytidiaceae (Ando et al., 1957; Koponen, 1971a), Sematophyllaceae (Iwatsuki, 1977a; Seki, 1968), Sphagnaceae (S.-h. Lin & Lai, 1981), Splachnaceae (Koponen & Koponen, 1974; Ochi et al., 1974), Thuidiaceae (Iwatsuki, 1963; Noguchi, 1964; Norris & Sharp, 1961; Watanabe, 1972, 1980a, 1980b), and Timmiaceae (Brassard, 1984).

Finally, "Index Muscorum" (Wijk et al., 1959–1969), "Index Muscorum Supplementum" (Crosby, 1977, 1979; Crosby & Bauer, 1981, 1983), and "Index Muscorum Japonicarum" (Iwatsuki & Noguchi, 1973, 1979) were useful in determining currently acceptable names and synonyms. Crosby and Magill (1977) were followed in assigning most genera to families.

The equal sign (=) is used to indicate both taxonomic and nomenclatural synonyms. Where some doubt exists about the status of a name, it is preceded by a question mark (?). Synonyms are restricted to those that have been specifically applied to the mosses of China.

We have refrained from making judgements as to the validity of the taxa reported for China. Some reports are undoubtedly based upon misidentifications or a lack of understanding of a taxon throughout its range. Since China borders

[1] The senior author wishes to express his thanks to Dr. Z. Iwatsuki for taking the time to discuss with him some of the problems associated with the preparation of this catalog and for suggesting some additional taxa, deletions, and synonyms and to Dr. H. Ando for going over the taxa in the Hypnaceae. Particular gratitude is due my colleague Dr. Wu who spent many hours working on this catalog. Finally, the authors are grateful to Cheryl Bauer for a critical review and editing of this paper. Financial and logistical support for the senior author is acknowledged to the Institute of Botany, Academia Sinica, Beijing; the Missouri Botanical Garden; and Southwest Missouri State University.

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on As 1 (Northern Asia), and As 3 (India, Burma, Indochina) and has historical biogeographical affinities with North America (Iwatsuki & Sharp, 1967, 1968), one may expect that when careful comparative studies are made of many taxa throughout their range in Asia and North America, a large number will be reduced to synonyms. Furthermore, because China encompasses 60 degrees of longitude and 38 degrees of latitude (17–55 degrees N) and varies in elevation from sea level along the coasts to 7,556 m in western Sichuan, its plant communities are diverse, ranging from alpine tundra to tropical rain forests and from deserts to temperate deciduous forests (Hou, 1983). Consequently, future field work should produce additional taxa for China.

LIST OF TAXA

Abietinella C. Müll. (THUIDIACEAE)
abietina (Hedw.) Fleisch.
histricosa (Mitt.) Broth.
Acanthocladium Mitt. (SEMATOPHYLLACEAE)
benguetense Broth. = *Wijkia benguetensis*
juliforme Herz. & Dix. ex Dix.
sublepidum Broth.
tanytrichum (Mont.) Broth. in Par. = *Wijkia tanytricha*
Acanthorrhynchium Fleisch. (SEMATOPHYLLACEAE)
papillatum (Harv.) Fleisch.
Acaulon C. Müll. (POTTIACEAE)
muticum (Hedw.) C. Müll.
Acroporium Mitt. (SEMATOPHYLLACEAE)
diminutum (Brid.) Fleisch.
flagelliferum Sak. = *Neacroporium flagelliferum*
hyalinum Mitt. = *A. stramineum*
oxyporum (Lac.) Fleisch.
stramineum (Reim. & Hornsch.) Fleisch.
suzukii Sak.
turgidum Mitt.
Actinodontium Schwaegr. in Hedw. (DALTONIACEAE)
rhaphidostegum (C. Müll.) Bosch. & Lac.
Actinothuidium (Besch.) Broth. (THUIDIACEAE)
hookeri (Mitt.) Broth.
Aerobryidium Fleisch. in Broth. (METEORIACEAE)
aureo-nitens (Schwaegr.) Broth.
filamentosum (Hook.) Fleisch. in Broth.
taiwanense Nog.
Aerobryopsis Fleisch. (METEORIACEAE)
(?) *auriculata* Copp. ex. Thér.
brevicuspis Broth. = *Pseudobarbella attenuata*
hokinensis (Besch.) Broth.
horrida Nog. = *A. subdivergens* ssp. *scariosa*
integrifolia (Besch.) Broth.
longissima (Dozy & Molk.) Fleisch. = *A. wallichii*
parisii (Card.) Broth.
subdivergens (Broth.) Broth. ssp. *subdivergens*
ssp. *scariosa* (Bartr.) Nog.
var. robusta Card. = *A. subdivergens* ssp. *subdivergens*
wallichii (Brid.) Fleisch.
Aerobryum Dozy & Molk. (METEORIACEAE)
speciosum (Dozy & Molk.) Dozy & Molk.
Aloina Kindb. (POTTIACEAE)
aloides (K. Schultz) Kindb.
ericaefolia (Lindb.) Kindb. = *A. rigida* var. *ambigua*
obliquifolia (C. Müll.) Broth.
rigida (Hedw.) Limpr. var. *rigida*
var. *ambigua* (B.S.G.) Craig ex Sayre
Amblystegiella Loeske (AMBLYSTEGIACEAE)
jungermannioides (Brid.) Giac. = *Platydictya jungermannioides*
sinensi-subtilis (C. Müll.) Broth.
sprucei (Bruch) Loeske = *Platydictya jungermannioides*
yuennanensis Broth.
Amblystegium B.S.G. (AMBLYSTEGIACEAE)
campyliopsis Dix.
juratzkanum Schimp. = *A. serpens* var. *juratzkanum*
kochii B.S.G. = *A. trichopodium*
noterophilum (Sull. & Lesq. ex Sull.) Holz.
riparium (Hedw.) B.S.G.
serpens (Hedw.) B.S.G. var. *serpens*
ssp. rigescens (Limpr.) Meyl. = *A. serpens*
var. *juratzkanum* (Schimp.) Rau & Herv.
var. *rigidiusculum* Lindb. & Arn.
tenax (Hedw.) C. Jens.
trichopodium (K. Schultz) Hartm.
varium (Hedw.) Lindb.
Amphidium Schimp. (ORTHOTRICHACEAE)
lapponicum (Hedw.) Schimp.
mougeotii (B.S.G.) Schimp. var. *mougeotii*
var. *formosicum* Card.
papillosum Bartr.
sublapponicum (C. Müll.) Broth.
Anacamptodon Brid. (FABRONIACEAE)
amblystegioides Card.
fortunei Mitt.
latidens (Besch.) Broth.
splachnoides (Brid.) Brid.
sublatidens Card.
subulatus Broth.
Anacolia Schimp. (BARTRAMIACEAE)
laevisphaera (Tayl.) Flow. in Grout
sinensis Broth.
webbii (Mont.) Schimp.
Andreaea Hedw. (ANDREAEACEAE)
amurensis Broth. in Fedtch.
densifolia Mitt.
fauriei Besch. = *A. rupestris* var. *fauriei*
hohuanensis Chuang
likiangensis Chen in Chen & Wan
mamillosula Chen in Chen & Wan
morrisonensis Nog.
obovata Thed.
rothii Web. & Mohr
rupestris Hedw. var. *rupestris*
var. *fauriei* (Besch.) Tak.
wangiana Chen in Chen & Wan
wilsonii Hook. f.
yuennanensis Broth.
Anisothecium Mitt. (DICRANACEAE)
palustre (Dicks.) I. Hag. = *Dicranella palustris*
rotundatum Broth. = *Dicranella rotundata*
rubrum Lindb. = *Dicranella varia*
varium (Hedw.) Mitt. = *Dicranella varia*
Anoectangium Schwaegr. (POTTIACEAE)

aestivum (Hedw.) Mitt.
clarum Mitt.
crassinervium Mitt.
euchloron (Schwaegr.) Mitt.
kweichowense Bartr. = *A. thomsonii*
latifolium Broth. = *A. clarum*
perminutum Broth. = *A. stracheyanum* var. *stracheyanum*
stracheyanum Mitt. var. *stracheyanum*
var. gymnostomoides (Broth. & Yas.) Wijk & Marg. = *A. stracheyanum* var. *stracheyanum*
subpulvinatum Broth. = *A. thomsonii*
thomsonii Mitt.
tortifolium Jaeg. = *A. stracheyanum* var. *stracheyanum*
Anomobryum Schimp. (BRYACEAE)
alpinum Zang & X.-j. Li in X.-j. Li (editor)
concinnatum (Spruce) Lindb. = *A. filiforme* ssp. *concinnatum*
filiforme (Dicks.) Solms in Rabenh. ssp. *filiforme*
ssp. *concinnatum* (Spruce) Amann
ssp. *juliforme* (Solms) Loeske
gemmigerum Broth.
nitidum (Mitt.) Jaeg.
proligerum Broth. & Herz.
tenerrimum Broth.
validum Dix.
yasudae Broth.
Anomodon Hook. & Tayl. (THUIDIACEAE)
abbreviatus Mitt.
acutifolius Mitt.
attenuatus (Hedw.) Hüb.
dentatus Gao
giraldii C. Müll.
grandiretus Broth.
integerrimus Mitt. = *A. minor* ssp. *integerrimus*
longifolius (Brid.) C. J. Hartm.
minor (Hedw.) Fürnr. ssp. *minor*
ssp. *integerrimus* (Mitt.) Iwats.
rotundatus Par. & Broth.
rugelii (C. Müll.) Keissl.
sinensis C. Müll. = *A. minor* ssp. *minor*
thraustus C. Müll.
viticulosus (Hedw.) Hook. & Tayl.
Antitrichia Brid. (LEUCODONTACEAE)
curtipendula (Hedw.) Brid.
formosana Nog.
Aongstroemia B.S.G. (DICRANACEAE)
orientalis Mitt.
uncinifolia (Broth.) Broth. = *A. orientalis*
Aongstroemiopsis Fleisch. (DICRANACEAE)
julacea (Dozy & Molk.) Fleisch.
Aptychella (Broth.) Herz. (SEMATOPHYLLACEAE)
brevinervis (Fleisch.) Fleisch.
delicata (Fleisch.) Fleisch.
glomerato-propagulifera (Toyama) Seki
handelii Broth.
heteroclada (Fleisch.) Fleisch.
planula (Mitt.) Fleisch.
proligera (Broth.) Herz.
robusta (Broth.) Fleisch.
subdelicata Broth.
yuennanensis Broth.
Archidium Brid. (ARCHIDIACEAE)
alternifolium (Hedw.) Mitt. [Not included in As 2 by Snider, 1975]
ohioense Schimp. ex. C. Müll.
sinense Dur. in Debeaux = (?) *A. ohioense* [Snider, 1975]
Arctoa B.S.G. (DICRANACEAE)
fulvella (Dicks.) B.S.G.
hyperborea (With.) B.S.G.
Astomiopsis C. Müll. (DITRICHACEAE)
amblyocalyx C. Müll.
sinensis Broth.
Astomum Hampe (POTTIACEAE)
crispum (Hedw.) Hampe = *Weissia crispa*
Atractylocarpus Mitt. (DICRANACEAE)
alpinus (Milde) Lindb.
sinensis (Broth.) Herz.
Atrichum P. Beauv. (POLYTRICHACEAE)
angustatum (Brid.) B.S.G. var. *angustatum* [Not included in As 2 by Nyholm, 1971]
var. rhystophyllum (C. Müll.) Richards & Wallace = *A. rhystophyllum*
crispulum Schimp. ex. Besch.
crispum (James) Sull. & Lesq. [Not included in As 2 by Nyholm, 1971]
gracile (C. Müll.) Par. = *A. pallidum* var. *gracile*
haussknechtii Jur. & Milde = *A. undulatum* var. *gracilisetum*
henryi (Salm.) Bartr.
obtusulum (C. Müll.) Jaeg.
pallidum Ren. & Card. var. *gracile* (C. Müll.) Nyh.
rhystophyllum (C. Müll.) Par.
speciosum (Horik.) Wijk & Marg.
spinulosum (Card.) Miz. = *A. crispulum*
undulatum (Hedw.) P. Beauv. var. *undulatum*
var. *gracilisetum* Besch.
var. haussknechtii (Jur. & Milde) Frye in Grout = *A. undulatum* var. *gracilisetum*
var. minus (Hedw.) Par. = *A. rhystophyllum*
var. *subserratum* (Hook.) Par.
yakushimense (Horik.) Mizush.
yuennanense (Broth.) Bartr. = (?) *A. undulatum* var. *gracilisetum* [Nyholm, 1971]
Aulacomnium Schwaegr. (AULACOMNIACEAE)
androgynum (Hedw.) Schwaegr.
heterostichum (Hedw.) B.S.G.
palustre (Hedw.) Schwaegr. ssp. *palustre*
ssp. *imbricatum* (B.S.G.) Kindb.
turgidum (Wahlenb.) Schwaegr.
Aulacopilum Wils. (ERPODIACEAE)
abbreviatum Mitt.
japonicum Broth. ex Card.
Baldwiniella Broth. ex Fleisch. (NECKERACEAE)
tibetana Gao in Gao & K.-c. Chang
Barbella Fleish. in Broth. (METEORIACEAE)
asperifolia Card. = *B. flagellifera*
biformis Nog.
chrysonema (C. Müll.) Nog.
compressiramea (Ren. & Card.) Fleisch. in Broth.
enervis (Thwaites & Mitt.) Fleisch. ex Broth.
flagellifera (Card.) Nog.
pendula (Sull.) Fleisch.
pilifera Broth. & Yas. = *Neobarbella pilifera*
rufifolioides (Broth.) Broth.
Barbellopsis Broth. (METEORIACEAE)
sinensis Broth. = *Barbella enervis*
Barbula Hedw. (POTTIACEAE)
anserino-capitata X.-j. Li

asperfolia Mitt. = *Didymodon asperfolius*
constricta Mitt. var. *constricta*
var. *flexicuspis* Chen
convoluta Hedw. = *Streblotrichum convolutum*
cruegeri Sond. ex C. Müll.
defossa C. Müll. = *B. tectorum*
ditrichoides Broth.
fallax Hedw. = *Didymodon fallax*
gigantea Funck
gracillima (Herz.) Broth.
indica (Hook.) Spreng. in Steud.
javanica Dozy & Molk. = *Hydrogonium javanicum*
longicostata X.-j. Li
nigrescens Mitt.
pallido-basis Dix.
perobtusa (Broth.) Chen
reflexa (Brid.) Brid. = *Didymodon rigidicaulis*
rigidula (Hedw.) Milde var. rigidula = *Didymodon rigidulus*
var. perobtusa Broth. = *B. perobtusa*
rivicola Broth. = *Didymodon rivicola*
rufa (Lor.) Jur. = *Didymodon asperifolius*
schensiana C. Müll. = *Didymodon vinealis*
subcomosa Broth.
subcontorta Broth.
subrivicola Chen var. *subrivicola*
var. *densifolia* Chen
tectorum C. Müll.
tenii Herz.
tophacea (Brid.) Mitt. = *Didymodon tophaceus*
unguiculata Hedw. var. *unguiculata*
var. *trichostomifolia* (C. Müll.) Chen
vinealis Brid. = *Didymodon vinealis*

Bartramia Hedw. (BARTRAMIACEAE)
halleriana Hedw.
ithyphylla Brid.
norvegica Lindb. = *B. halleriana*
pomiformis Hedw. ex Okam. var. *pomiformis*
var. *elongata* Turn.
subulata B.S.G.
viridissima (Brid.) Kindb. = *B. subulata*

Bartramidula B.S.G. (BARTRAMIACEAE)
bartramioides (Griffith) Wijk & Marg.
cernua Lindb.
roylei (Hook. f.) B.S.G.
wilsonii B.S.G. = *B. cernua*

Bellibarbula Chen (POTTIACEAE)
kurziana Chen
obtusicuspis (Besch.) Chen

Blindia B.S.G. (SELIGERIACEAE)
acuta (Hedw.) B.S.G. var. *acuta*
var. *japonica* (Broth.) Gao
seligerioides Lindb. ex Broth.

Boulaya Card. (THUIDIACEAE)
mittenii (Broth.) Card.

Brachymeniopsis Broth. (FUNARIACEAE)
gymnostoma Broth.

Brachymenium Schwaegr. (BRYACEAE)
acuminatum Harv. in Hook.
contortum Hampe ex Ochi = *B. ochianum*
crassinervium Broth.
exile (Dozy & Molk.) Bosch & Lac.
immarginatum Gao & K.-c. Chang
jilinense T. Kop., Shaw, Lou & Gao
muricola Broth.
nepalense Hook. in Schwaegr. var. *nepalense*
var. *clavulum* (Mitt.) Ochi
ochianum Gang.
parvulum Broth.
ptychothecium (Besch.) Ochi
sinense Card. & Thér.

Brachythecium B.S.G. (BRACHYTHECIACEAE)
albicans (Hedw.) B.S.G.
amnicola C. Müll.
brotheri Par.
buchananii (Hook.) Jaeg. var. *buchananii*
var. *gracillimum* Dix.
campestre (C. Müll.) B.S.G.
camptothecioides Tak.
campylothallum C. Müll.
collinum (C. Müll.) B.S.G.
dicranoides C. Müll.
fasciculirameum C. Müll.
formosanum Tak.
garovaglioides C. Müll.
glaciale B.S.G.
glareosum (Spruce) B.S.G.
glauco-viride C. Müll.
glauculum C. Müll.
kuroishicum Besch.
longinerve Broth. = *Bryhnia novae-angliae*
oedistegum (C. Müll.) Jaeg.
perminusculum C. Müll.
permolle C. Müll.
perscabrum Broth.
piliferum (Hedw.) Kindb. = *Cirriphyllum piliferum*
piligerum Card.
pinnatum Tak.
pinnirameum C. Müll.
planiusculum C. Müll.
plumosum (Hedw.) B.S.G. var. *plumosum*
var. *densirete* (Broth. & Par.) Tak.
var. *mimmayae* Card.
var. *nitidum* (Sak.) Tak.
var. *scabrum* Broth.
populeum (Hedw.) B.S.G. var. *populeum*
var. *japonicum* Dix. & Thér.
var. *quelpaertense* (Card.) Tak.
var. *yamamotoi* (Sak.) Tak.
procumbens (Mitt.) Jaeg.
pygmaeum Tak.
quelpaertense Card. = *B. populeum* var. *quelpaertense*
reflexum (Starke) B.S.G.
rhynchostegielloides Card. var. *rhynchostegielloides*
var. macrocarpum Card. = *B. rhynchostegielloides*
rivulare B.S.G. var. *rivulare*
var. *gracile* Broth.
rutabulum (Hedw.) B.S.G.
sakuraii Broth.
salebrosum (Web. & Mohr) B.S.G.
sapporense (Besch.) Tak.
starkei (Brid.) B.S.G.
subcurvatulum Broth.
thraustum C. Müll.
uncinifolium Broth. & Par. = *Cratoneurella uncinifolia*
velutinum (Hedw.) B.S.G.
viridefactum C. Müll.
wichurae (Broth.) Par.
yamamotoi Sak. = *B. populeum* var. *yamamotoi*
yuennanense Herz.

Braunia B.S.G. (HEDWIGIACEAE)
alopecura (Brid.) Limpr.
delavayi Besch.
obtusicuspis Broth.
Breidleria Loeske = *Hypnum* (HYPNACEAE)
arcuata (Mol.) Loeske = *Hypnum lindbergii*
Breutelia (B.S.G.) Schimp. (BARTRAMIACEAE)
arundinifolia (Duby) Fleisch.
dicranacea (C. Müll.) Mitt.
setschwanica Broth. = *B. dicranacea*
subdeflexa Broth.
yunnanensis Besch.
Brothera C. Müll. (DICRANACEAE)
leana (Sull.) C. Müll.
Brotherella Loeske ex Fleisch. (SEMATOPHYLLACEAE)
erythrocaulis (Mitt.) Fleisch.
falcata (Dozy & Molk.) Fleisch.
falcatula Broth.
fauriei (Card.) Broth.
formosana Broth.
handelii Broth.
henonii (Duby) Fleisch.
himalayana Chen (nom. nud.) = *Pylaisiadelpha himalayana*
integrifolia Broth.
kirishimensis Sak.
lorentziana (Lor.) Loeske in Fleisch.
nictans (Mitt.) Broth.
piliformis Broth.
subintegra Broth.
yokohamae (Broth.) Broth.
Bruchia Schwaegr. (DICRANACEAE)
sinensis Chen (nom. nud.)
Bryhnia Kaur. (BRACHYTHECIACEAE)
higoensis Tak. = *B. novae-angliae*
hultenii Bartr. in Grout = *B. novae-angliae*
nitida Sak. = *Brachythecium plumosum* var. *nitidum*
novae-angliae (Sull. & Lesq.) Grout
stokesii (Turn.) Robins. = *Kindbergia praelongia*
sublaevifolia Broth. & Par. in Card.
Bryochenea Gao & K.-c. Chang (THUIDIACEAE)
ciliata Gao & K.-c. Chang
sachalinensis (Lindb.) Gao & K.-c. Chang
Bryoerythrophyllum Chen (POTTIACEAE)
alpigenum (Vent.) Chen
atrorubens (Besch.) Chen = *Didymodon atro-rubens*
brachystegium (Besch.) K. Saito
dentatum (Wils.) Chen
gymnostomum (Broth.) Chen
hostile (Herz.) Chen
obtusissimum (Broth.) Chen = *B. brachystegium*
pergemmascens (Broth.) Chen
recurvirostre (Hedw.) Chen
rubrum (Geh.) Chen
tenerrimum (Broth.) Chen
wallichii (Mitt.) Chen
yichunense (Herz.) Gao
yunnanense (Herz.) Chen
Bryohaplocladium Watan. & Iwats. (THUIDIACEAE)
angustifolium (Hampe & C. Müll.) Watan. & Iwats.
microphyllum (Hedw.) Watan. & Iwats.
Bryonoguchia Iwats. & H. Inoue (THUIDIACEAE)
molkenboeri (Lac.) Iwats. & H. Inoue
Bryosedgwickia Card. & Dix. (HYPNACEAE)
entodontea (C. Müll.) Fleisch.
Bryoxiphium Mitt. (BRYOXIPHIACEAE)
norvegicum (Brid.) Mitt. ssp. *japonicum* (Berggr.) A. Löve & D. Löve
Bryum Hedw. (BRYACEAE)
alpicola Broth.
alpinum Huds. ex With. var. *alpinum*
var. *teretiusculum* (Hook.) Podp.
ambiguum Duby in Moritzi = *B. plumosum*
andrei Card. & P. de la Varde
angustirete Kindb.
archangelicum B.S.G.
arcticum (R. Br.) B.S.G.
argenteum Hedw. var. *argenteum*
var. *lanatum* (P. Beauv.) Hampe
atrovirens Vill. ex. Brid.
badhwarii Ochi in Nog.
barbuloides Broth.
bicolor Dicks.
billardieri Schwaegr.
blandum Hook. f. & Wils. ssp. *handelii* (Broth.) Ochi
bulbiforme Broth.
caespiticium Hedw.
calophyllum R. Br. ssp. *calophyllum*
capillare Hedw.
cellulare Hook. in Schwaegr.
cernuum (Hedw.) B.S.G. = *B. uliginosum*
chrysobasilare Broth.
chrysobasillioides Broth.
chungii Bartr.
cirrhatum Hoppe & Hornsch. = *B. lonchocaulon*
compressidens C. Müll. = *B. cellulare*
coronatum Schwaegr.
cyclophyllum (Schwaegr.) B.S.G. = *B. tortifolium*
fortunatii Thér. = (?) *B. truncorum*
funkii Schwaegr.
giganteum (Schwaegr.) Arnott = *Rhodobryum ganteum*
globicoma C. Müll.
globosum Lindb. = *B. wrightii*
gossypinum Lee & Zang in Gao & K.-c. Chang
handelii Broth. = *B. blandum* ssp. *handelii*
japonense (Besch.) Broth. = *B. cellulare*
knowltonii Barnes
leptocaulon Card.
leucophylloides Broth.
lonchocaulon C. Müll.
longisetum Bland. ex Schwaegr.
neelgheriense Mont. in C. Müll. var. *neelgheriense*
var. *wichurae* (Broth.) Mohamed
neodamense Itzig. in C. Müll. var. *neodamense*
var. *ovatum* Lindb. & Arn.
nitens Hook. = *B. plumosum*
pallens Sw.
pallescens Schleich. ex Schwaegr. var. *pallescens*
var. *subrotundum* (Brid.) B.S.G.
paradoxum Schwaegr.
petelotii Thér. & Henry
plumosum Dozy & Molk.
porphyroneuron C. Müll.
pseudo-alpinum Ren. & Card. = *B. paradoxum*
pseudotriquetrum (Hedw.) Gaertn., Meyer & Schreb.
ssp. *pseudotriquetrum* var. *pseudotriquetrum*
var. *gracilens* (Card.) Ochi
ssp. *crispulum* (G. Roth) C. Jens.
ptychothecium Besch. = *B. ramosum*
pulchroalare Broth. = *B. blandum* ssp. *handelii*
purpurascens (R. Br.) B.S.G.

ramosum (Hook.) Mitt.
recurvulum Mitt.
retusifolium Card. & P. de la Varde
rubigineum C. Müll.
rutilans Brid.
salakense Card.
sauteri B.S.G.
schleicheri Schwaegr. = *B. turbinatum*
setschwanicum Broth.
simulans Broth.
sinense Mohamed
splachnoides (Harv.) C. Müll. = *B. cellulare*
thomsonii Mitt.
tibetanum Mitt.
tortifolium Brid.
truncorum (Brid.) Brid.
tsanii C. Müll. ex Iis.
turbinatoides Broth.
turbinatum (Hedw.) Turn.
uliginosum (Brid.) B.S.G.
ventricosum Relh. var. vestitum Broth. = *B. pseudotriquetrum* ssp. *pseudotriquetrum* var. *vestitum* Broth.
warneum (Röhl.) Brid.
wichurae Broth. = *B. neelgheriense* var. *wichurae*
wrightii Sull. & Lesq.
yuennanense Broth. = *B. capillare*

Buxbaumia Hedw. (BUXBAUMIACEAE)
aphylla Hedw.
indusiata Brid.
javanica C. Müll.
punctata Chen & Lee
symmetrica Chen & Lee

Callicladium Crum (SEMATOPHYLLACEAE)
haldanianum (Grev.) Crum

Callicostella (C. Müll.) Mitt. (HOOKERIACEAE)
papillata (Mont.) Mitt.

Calliergon (Sull.) Kindb. (AMBLYSTEGIACEAE)
cordifolium (Hedw.) Kindb.
giganteum (Schimp.) Kindb.
sarmentosum (Wahlenb.) Kindb.
stramineum (Brid.) Kindb.
turgescens (T. Jens.) Kindb. = *Scorpidium turgescens*

Calliergonella Loeske (AMBLYSTEGIACEAE)
cuspidata (Hedw.) Loeske

Calymperes Sw. in Web. (CALYMPERACEAE)
cristatum Hampe
cuculatum P.-j. Lin
dozyanum Mitt.
erosum C. Müll.
fasciculatum Dozy & Molk.
fordii Besch. = *C. thwaitesii* ssp. *fordii*
hampei Dozy & Molk. = *C. erosum*
japonicum Besch. = *Syrrhopodon japonicus*
johannis-winkleri Broth. var. hasegawae (Tak. & Iwats.) Iwats. = *C. fasciculatum*
lonchophyllum Schwaegr.
longifolium Mitt.
serratum A. Br. ex C. Müll.
strictifolium (Mitt.) G. Roth
tahitense (Sull.) Mitt.
tenerum C. Müll.
thwaitesii Besch. ssp. *fordii* (Besch.) Fleisch.
tuberculosum (Thér. & Dix.) Broth. = *C. strictifolium*

Calymperopsis (C. Müll.) Fleisch. (CALYMPERACEAE)
involuta P.-j. Lin
semiliber (Mitt.) Fleisch.
tjibodensis (Fleisch.) Fleisch.
yunfuensis Wu, Lou & Men

Calyptothecium Mitt. (PTEROBRYACEAE)
acostatum Lou
caudatum Bartr.
cuspidatum (Okam.) Nog. var. *cuspidatum* var. *laxifolium* Nog.
formosanum Broth.
hookeri (Mitt.) Broth.
japonicum Thér. = *C. urvilleanum*
nitidum (Ren. & Card.) Fleisch.
pinnatum Nog.
stricticaulon Lou
subacuminatum (Broth. & Par.) Broth.
tumidum (Dicks.) Fleisch. = *C. urvilleanum*
urvilleanum (C. Müll.) Broth.
wightii (Mitt.) Fleisch.

Calyptrochaeta Desv. (HOOKERIACEAE)
japonica (Card. & Thér.) Iwats. & Nog.
parviretis (Fleisch.) Iwats., Tan & Touw in Touw
spinosa (Nog.) Ninh

Camptochaete Reich. (LEMBOPHYLLACEAE)
arbuscula (J. Sm.) Reich.
sinensis Broth. var. *sinensis*
var. *flagellifera* (Broth.) Redf. & Wu, comb. nov.
Isotheciopsis sinensis var. *flagellifera* Broth., Symb. Sin. 4: 90. 1929.

Camptothecium B.S.G. (BRACHYTHECIACEAE)
auriculatum (Jaeg.) Broth.
lutescens (Hedw.) B.S.G.

Campyliadelphus (Kindb.) R. Chopra = *Campylium* (AMBLYSTEGIACEAE)
chrysophyllus (Brid.) Kanda = *Campylium chrysophyllum*
stellatus (Hedw.) Kanda = *Campylium stellatum*

Campylium (Sull.) Mitt. (AMBLYSTEGIACEAE)
amblystegioides Broth.
chrysophyllum (Brid.) J. Lange var. *chrysophyllum* var. *zemliae* (C. Jens.) Grout
courtoisii Par. & Broth.
enerve Herz. & Nog.
hispidulum (Brid.) Mitt. var. *hispidulum* var. *sommerfeltii* (Myr.) Lindb.
polygamum (B.S.G.) C. Jens. var. *polygamum* var. *stagnatum* (Wils.) Dix.
porphyriticum C. Müll.
protensum (Brid.) Kindb.
serratifolium (Card.) Herz. & Nog.
sommerfeltii (Myr.) J. Lange = *C. hispidulum* var. *sommerfeltii*
stellatum (Hedw.) C. Jens.
uninervium C. Müll. var. *uninervium* var. *minus* C. Müll.

Campylodontium Dozy & Molk. = *Mesonodon* (ENTODONTACEAE)
flavescens (Hook.) Bosch & Lac. = *Mesonodon flavescens*

Campylophyllum (Schimp.) Fleisch. (AMBLYSTEGIACEAE)
halleri (Hedw.) Fleisch.

Campylopodium (C. Müll.) Besch. (DICRANACEAE)
euphorocladum (C. Müll.) Besch.

Campylopus Brid. (DICRANACEAE)

alpigena Broth. var. *alpigena*
var. *lamellatus* Broth.
atro-virens De Not.
aureus Bosch & Lac.
caudatus (C. Müll.) Mont. in Dozy & Molk.
flexuosus (Hedw.) Brid.
fragilis (Brid.) B.S.G. var. *fragilis*
var. *pyriformis* (K. Schultz) Ångstr.
fuscoviridis (Card.) Dix. & Thér. ex Hong & Ando
gracilentus Card.
gracilis (Mitt.) Jaeg.
handelii Broth. var. *handelii*
var. *setschwanicus* Broth.
irrigatus Thér.
japonicus Broth.
latinervis (Mitt.) Jaeg.
laxitextus Lac.
longigemmatus Gao in Gao, G.-c. Zhang & Cao
pinfaensis Thér.
pyriformis (K. Schultz) Brid. = *C. fragilis* var. *pyriformis*
richardii Brid.
scabridorsus Dix.
schimperi Milde = *C. subulatus* var. *schimperi*
schwarzii Schimp.
setifolius Wils.
subulatus Schimp. in Rabenh. var. *subulatus*
var. *schimperi* (Milde) Husn.
taiwanensis Sak.
tenuinervis Fleisch.
umbellatus (Arnott) Par.
zollingerianus (C. Müll.) Bosch & Lac.
Catharinea Web. & Mohr = *Atrichum* (POLYTRICHACEAE)
henryi Salm. = *Atrichum henryi*
yuennanensis Broth. = *Atrichum undulatum* var. *gracilisetum*
var. minor Broth. = *Atrichum rhystophyllum*
Catoscopium Brid. (CATOSCOPIACEAE)
nigritum (Hedw.) Brid.
Ceratodon Brid. (DITRICHACEAE)
purpureus (Hedw.) Brid. var. *purpureus*
var. *formosicus* Card.
var. *rotundifolius* Berggr.
stenocarpus Bruch & Schimp. ex C. Müll.
Chaetomitriopsis Fleisch. (HOOKERIACEAE)
glaucocarpa (Schwaegr.) Fleisch.
Chaetomitrium Dozy & Molk. (HOOKERIACEAE)
acanthocarpum Bosch & Lac.
orthorrhynchum (Dozy & Molk.) Bosch & Lac.
Chionostomum C. Müll. (SEMATOPHYLLACEAE)
rostratum (Griffith) C. Müll. var. *rostratum*
var. *microcarpum* Broth.
Chrysocladium Fleisch. (METEORIACEAE)
flammeum (Mitt.) Fleisch. ssp. *flammeum*
ssp. *ochraceum* (Nog.) Nog.
kiusiuense (Broth. & Par.) Fleisch. = *C. retrorsum*
phaeum (Mitt.) Fleisch.
retrorsum (Mitt.) Fleisch. var. *retrorsum*
var. pinnatum Card. ex Nog. = *C. retrorsum*
var. taiwanense Nog. = *C. retrorsum*
robustum Nog. = *C. phaeum*
Cinclidium Sw. in Schrad. (MNIACEAE)
arcticum Schimp.
stygium Sw. in Schrad.
Cinclidotus P. Beauv. (POTTIACEAE)
fontinaloides (Hedw.) P. Beauv.
Cirriphyllum Grout (BRACHYTHECIACEAE)
cirrhosum (Schwaegr. ex Schultes) Grout
crassinervium (Tayl.) Loeske & Fleisch.
piliferum (Hedw.) Grout
subnerve Dix.
Claopodium (Lesq. & James) Ren. & Card. (THUIDIACEAE)
aciculum (Broth.) Broth.
assurgens (Sull. & Lesq.) Card.
crispifolium (Hook.) Ren. & Card.
fulvellum Herz.
gracillimum (Card. & Thér.) Nog.
integrum Chen ex Wu, Lou & M.-z. Wang (nom. nud.)
nervosum (Harv.) Fleisch. = *C. prionophyllum*
papillicaule (Broth.) Broth. = *C. pellucinerve*
pellucinerve (Mitt.) Best
piliferum Broth. = *C. pellucinerve*
prionophyllum Broth.
rugulosifolium Zeng
sinicum Broth. & Par. = *C. aciculum*
Clastobryella Fleisch. (SEMATOPHYLLACEAE)
cuculligera (Lac.) Fleisch.
glomerato-propagulifera (Toyama) Seki = *Aptychella glomerato-propagulifera*
kusatsuensis (Besch.) Iwats. = *Brotherella yokohamae*
tenerrima Broth.
tsunodae (Broth. & Yas.) Broth. = *Brotherella yokohamae*
Clastobryum Dozy & Molk. (SEMATOPHYLLACEAE)
excavatum Broth.
indicum (Dozy & Molk.) Dozy & Molk.
katoi Broth. = *Oedicladium rufescens*
sinense Dix.
Cleistostoma Brid. = *Syrrhopodon* (CALYMPERACEAE)
ambiguum (Hook.) Brid. = *Syrrhopodon ambiguus*
Climacium Web. & Mohr (CLIMACIACEAE)
americanum Brid. ssp. japonicum (Lindb.) J. Perss. = *C. japonicum*
dendroides (Hedw.) Web. & Mohr
japonicum Lindb.
Cratoneurella Robins. (BRACHYTHECIACEAE)
uncinifolia (Broth. & Par.) Robins.
Cratoneuron (Sull.) Spruce (AMBLYSTEGIACEAE)
commutatum (Hedw.) G. Roth var. *commutatum*
var. falcatum (Brid.) Moenk. = *C. commutatum* var. *sulcatum* (Lindb.) Mönk.
curvicaule (Jur.) G. Roth = *C. filicinum* var. *curvicaule*
falcatum (Brid.) G. Roth var. falcatum = *C. commutatum*
filicinum (Hedw.) Spruce var. *filicinum*
var. *curvicaule* (Jur.) Mönk.
var. fallax (Brid.) G. Roth = *C. filicinum*
formosanum Broth.
Crossidium Jur. (POTTIACEAE)
chloronotos (Brid.) Limpr.
squamiferum (Viv.) Jur.
Cryphaea Web. (CRYPHAEACEAE)
heteromalla (Hedw.) Mohr in Web.
leveillei Thér.
sinensis Bartr.
Ctenidium (Schimp.) Mitt. (HYPNACEAE)

andoi Mishimura
capillifolium (Mitt.) Broth.
melacobolum (C. Müll.) Broth.
pinnatum (Broth. & Par.) Broth.
plumulosum Bartr. (hom. illeg.) = *C. pinnatum*
robusticaule Broth. & Par. = *C. capillifolium*
scaberrimum (Card.) Broth. var. scaberrimum = *Ectropothecium zollingeri*
serratifolium (Card.) Broth.
Cupressina C. Müll. = *Hypnum* (HYPNACEAE)
alaris C. Müll. = *Hypnum plumaeforme* var. *sinensi-molluscum*
leptothalla C. Müll. = *Eurohypnum leptothallum*
leucodontea C. Müll. = *Eurohypnum leptothallum*
minuta C. Müll. = *Hypnum shensianum*
sinensi-mollusca C. Müll. = *Hypnum plumaeforme* var. *sinensi-molluscum*
tereticaulis C. Müll. = *Eurohypnum leptothallum*
turgens C. Müll. = *Gollania turgens*
ulophylla C. Müll. = *Hypnum subimponens* ssp. *ulophyllum*
Cyathophorella (Broth.) Fleisch. (DALTONIACEAE)
densifolia Horik. = *C. hookeriana*
grandistipulacea Dix. & Sak.
hookeriana (Griffith) Fleisch.
intermedia (Mitt.) Broth.
kyusyuensis Horik. & Nog.
rigidula Chen (nom. nud.) = *C. hookeriana*
serrulata Chen (nom. nud.) = *C. tonkinensis*
spinosa (C. Müll.) Fleisch.
subspinosa Chen
taiwaniana Lai
tonkinensis (Broth. & Par.) Broth.
Cyclodictyon Mitt. (HOOKERIACEAE)
blumeanum (C. Müll.) Kuntze
laete-virens (Hook. & Tayl.) Mitt.
Cynodontium Schimp. (DICRANACEAE)
fallax Limpr.
gracilescens (Web. & Mohr) Schimp.
Cyrtomnium Holmen (MNIACEAE)
hymenophylloides (Hüb.) T. Kop.
Daltonia Hook. & Tayl. (DALTONIACEAE)
angustifolia Dozy & Molk. var. *angustifolia* var. *strictifolia* (Mitt.) Fleisch.
aristifolia Ren. & Card.
splachnoides (J. Sm.) Hook. & Tayl.
Dendrocyathophorum Dix. (HOOKERIACEAE)
intermedium (Mitt.) Herz.
Desmatodon Brid. (POTTIACEAE)
capillaris Chen
cernuus (Hüb.) B.S.G.
gemmascens Chen
latifolius (Hedw.) Brid. var. *latifolius* var. *muticus* (Brid.) Brid.
laureri (K. Schultz) B.S.G. var. *laureri* var. *setschwanicus* (Broth.) Chen
leucostoma (R. Br.) Berggr.
obtusifolius (Schwaegr.) Schimp. = *Tortula obtusifolia*
raucopapillosum X.-j. Li
suberectus (Hook.) Limpr. = *D. leucostoma*
systylius Schimp.
thomsonii (C. Müll.) Jaeg.
yuennanensis Broth.
Diaphanodon Ren. & Card. (TRACHYPODACEAE)
blandus (Harv.) Ren. & Card.
thuidioides Ren. & Card. = *D. blandus*
Dichodontium Schimp. (DICRANACEAE)
pellucidum (Hedw.) Schimp.
Dicranella (C. Müll.) Schimp. (DICRANACEAE)
austro-sinensis Herz. & Dix.
cerviculata (Hedw.) Schimp.
coarctata (C. Müll.) Bosch & Lac.
divaricatula Besch.
fukienensis Broth.
grevilleana (Brid.) Schimp.
heteromalla (Hedw.) Schimp.
leptoneura Dix.
liliputana (C. Müll.) Par.
micro-divaricata (C. Müll.) Par.
obscura Sull. & Lesq.
palustris (Dicks.) Crundw. ex E. Warb.
rotundata (Broth.) Tak.
squarrosa (Starke) Schimp. = *Dicranella palustris*
subulata (Hedw.) Schimp.
varia (Hedw.) Schimp.
Dicranodontium B.S.G. (DICRANACEAE)
asperulum (Mitt.) Broth.
attenuatum (Mitt.) Wils. ex Jaeg.
blindioides (Besch.) Broth. var. *blindioides* var. *robustum* Broth.
caespitosum (Mitt.) Par.
denudatum (Brid.) Britt. ex Williams
didictyon (Mitt.) Jaeg.
filifolium Broth.
nitidum (Dozy & Molk.) Fleisch.
papillifolium Gao in Gao, G.-c. Zhang & Cao
porodictyon Card. & Thér.
sinense (C. Müll.) Par.
subintegrifolium Broth.
subporodictyon Broth.
tenii Broth. & Herz.
uncinatum (Harv.) Jaeg.
Dicranoloma (Ren.) Ren. (DICRANACEAE)
assimile (Hampe) Par.
blumii (Nees) Par.
brevisetum (Dozy & Molk.) Par.
var. *samoanum* (Broth.) Tan & T. Kop.
f. *nematosum* (Broth. & Geh.) Tan & T. Kop.
cylindrothecium (Mitt.) Sak. = *D. subcylindrothecium*
dicarpum (Nees) Par.
formosanum Broth. = *D. assimile*
Dicranoweisia Lindb. ex Milde (DICRANACEAE)
cirrata (Hedw.) Lindb. ex Milde
crispula (Hedw.) Milde
indica (Wils.) Par.
Dicranum Hedw. (DICRANACEAE)
assamicum Dix.
bonjeanii De Not. in Lisa ssp. *bonjeanii* ssp. *angustum* (Lindb.) Podp.
caesium Mitt.
cheoi Bartr.
conanenum Gao in Gao & K.-c. Chang.
crispifolium C. Müll.
crispo-falcatum Schimp. ex Besch. = *D. hamulosum*
cylindricum Broth. (hom. illeg.)
delavayi Besch.
diplospiniferum Gao & Aur
drummondii C. Müll.
elongatum Schleich. ex Schwaegr. var. *elongatum* var. sphagni T. Jens. = *D. groelandicum*
flagellare Hedw.
fragilifolium Lindb.

fulvum Hook.
fuscescens Turn. ssp. *fuscescens*
ssp. *congestum* (Brid.) Kindb.
groenlandicum Brid.
gymnostomoides Broth. var. *gymnostomoides*
var. *microcarpum* Broth.
gymnostomun Mitt.
hamulosum Mitt.
handelii Broth.
himalayanum Mitt.
japonicum Mitt. var. *japonicum*
var. *yunnanense* Salm.
kashmirense Broth.
linzianum Gao in Gao & K.-c. Chang
lorifolium Mitt.
majus Turn.
mamillosum Gao & Aur
mayrii Broth.
muehlenbeckii B.S.G. var. *muehlenbeckii*
var. *neglectum* (De Not.) Pfeff.
nipponense Besch.
orthophyllum Broth.
papillidens Broth.
perfalcatum Broth. var. *perfalcatum* (hom. illeg.)
var. *latifolium* Broth.
perindutum Card. = *D. hamulosum*
polysetum Sw.
ramosum Gao & Aur
scoparium Hedw. var. *scoparium*
var. integrifolium Lindb. = *D. bonjeanii* ssp. *augustum*
scopellifolium C. Müll.
scottianum Turn.
kwangtungense Chen
subcylindrothecium Broth.
tibetanum Gao in Gao & K.-c. Chang
sericifolium Dix.
setschwanicum Broth.
spadiceum Zett. = *D. muehlenbeckii* var. *neglectum*
spurium Hedw.
tauricum Sap. = *Orthodicranum strictum*
thelinotum C. Müll.
truncicola Broth.
undulatum Schrad. ex Brid.
Didymodon Hedw. (POTTIACEAE)
asperifolius (Mitt.) Crum, Steere & Anderson
atro-rubens (Besch.) Broth. = *Bryoerythrophyllum wallichii*
constrictus (Mitt.) K. Saito var. constrictus = *D. vinealis*
var. flexicuspis (Chen) K. Saito = *D. vinealis*
cordatus Jur. = *Barbula gigantea*
eroso-denticulatus (C. Müll.) K. Saito
fallax (Hedw.) Zander
giganteus (Funck) Jur.
icmadophyllus (Schimp. ex C. Müll.) K. Saito
japonicus (Broth.) K. Saito
leskeoides K. Saito
nigrescens (Mitt.) K. Saito
rigidicaulis (C. Müll.) K. Saito
rigidulus Hedw. var. *rigidulus*
rivicola (Brid.) Zander in T. Kop., Gao, Lou & Järvinen
rubellus B.S.G. = *Bryoerythrophyllum recurvirostre*
rufidulus (C. Müll.) Broth.
submicrostomus Dix. = *Bryoerythrophyllum recurvirostre*
tectorum (C. Müll.) K. Saito
tophaceus (Brid.) Lisa
vinealis (Brid.) Zander
yunnanensis (Herz.) Broth. = *Bryoerythrophyllum yunnanense*
Diphyscium Mohr (DIPHYSCIACEAE)
foliosum (Hedw.) Mohr
formosicum Horik.
fulvifolium Mitt. var. *fulvifolium*
var. *leveillei* Thér. in Broth.
granulosum Chen
involutum Mitt.
macrophyllum C.-k. Wang & S.-h. Lin
rotundatifolium C.-k. Wang & S.-h. Lin
Distichium B.S.G. (DITRICHACEAE)
brevisetum Gao in Gao, G.-c. Zhang & Cao
bryoxiphioidium Gao in Gao, G.-c. Zhang & Cao
capillaceum (Hedw.) B.S.G.
hagenii Ryan ex Philib.
inclinatum (Hedw.) B.S.G.
macrosporum Gao in X-j. Li (editor)
Distichophyllum Dozy & Molk. (HOOKERIACEAE)
brevirostratum Thér.
cavaleriei Thér.
collenchymatosum Card.
cuspidatum (Dozy & Molk.) Dozy & Molk.
flavescens (Mitt.) Par.
jungermannioides (C. Müll.) Bosch & Lac.
maibarae Besch.
mittenii Bosch & Lac.
nigricaule Mitt. ex Bosch & Lac.
osterwaldii Fleisch.
sinense Dix. = *D. collenchymatosum*
stillicidiorum Broth.
Ditrichopsis Broth. (DITRICHACEAE)
clausa Broth.
gymnostoma Broth.
Ditrichum Hampe (DITRICHACEAE)
aureum Bartr.
brevidens Nog.
crispatissimum (C. Müll.) Par.
difficile (Duby) Fleisch.
divaricatum Mitt.
flexicaule (Schwaegr.) Hampe = *D. crispatissimum*
flexifolium Hampe = *D. difficile*
heteromallum (Hedw.) Britt.
homomallum (Hedw.) Hampe = *D. heteromallum*
microcarpum Broth.
pallidum (Hedw.) Hampe var. *pallidum*
var. *sinense* Thér.
pusillum (Hedw.) Hampe var. *pusillum*
var. *tortile* (Schrad.) I. Hag.
setschwanicum Broth.
tortile (Schrad.) Brockm. = *D. pusillum* var. *tortile*
Dolichomitra (Lindb.) Broth. (LEMBOPHYLLACEAE)
cymbifolia (Lindb.) Broth. var. *cymbifolia*
var. *subintegerrima* Okam.
Dolichomitriopsis Okam. (LEMBOPHYLLACEAE)
crenulata Okam.
diversiformis (Mitt.) Nog.
Dozya Lac. in Miquel (LEUCODONTACEAE)
japonica Sande-Lac. in Miquel
Drepanocladus (C. Müll.) G. Roth (AMBLYSTEGIACEAE)
aduncus (Hedw.) Warnst. var. *aduncus* f. *aduncus*
var. *kneiffi* (B.S.G.) Mönk.
var. *polycarpus* (Voit) G. Roth
f. *pseudofluitans* (Sanio) Mönk.

aomoriensis (Par.) Broth. = *Sasaokea aomoriensis*
cuspidarioides (C. Müll.) Broth. ex Par.
exannulatus (B.S.G.) Warnst. f. *exannulatus*
f. *angustissimus* Mönk.
fluitans (Hedw.) Warnst.
lycopodioides (Brid.) Warnst. var. *lycopodioides*
var. *abbreviatus* Mönk.
revolvens (Sw.) Warnst. f. *revolvens*
f. *cossonii* (Schimp.) Mönk.
sendtneri (Schimp.) Warnst. f. *sendtneri*
f. *borealis* (H. Arnell & C. Jens.) Mönk.
f. *trivalis* (Sanio) Mönk.
f. *wilsonii* (Lindb.) Mönk.
uncinatus (Hedw.) Warnst. f. *uncinatus*
f. *auriculatus* Mönk.
f. *longicuspis* Smirn.
f. *plumulosus* (Schimp.) Mönk.
vernicosus (Lindb.) Warnst.

Drummondia Hook. in Drumm. (ORTHOTRICHACEAE)
cavaleriei Thér.
obtusifolia C. Müll.
prorepens (Hedw.) Britt. var. *prorepens* [Not included in As 2 by Vitt, 1972]
var. *latifolia* Gao
rubiginosa C. Müll.
sinensis C. Müll.
thomsonii Mitt.

Duthiella C. Müll. in Broth. (TRACHYPODACEAE)
declinata (Mitt.) Zant.
flaccida (Card.) Broth. var. *flaccida*
var. *media* (Nog.) Zant.
var. *rigida* (Broth.) Zant.
formosana Nog.
media Nog. = *D. flaccida* var. *media*
pellucens Card. & Thér. = *D. flaccida* var. *flaccida*
perpapillata Broth. = *D. flaccida* var. *flaccida*
rigida Broth. = *D. flaccida* var. *rigida*
robusta Nog.
speciosissima Broth. ex Card.
wallichii (Mitt.) C. Müll. in Broth.

Ectropotheciella Fleisch. (HYPNACEAE)
distichophylla (Hampe) Fleisch.

Ectropothecium Mitt. (HYPNACEAE)
buitenzorgii (Bél.) Mitt.
circinatum Bartr. = *Hypnum plumaeforme*
dealbatum (Reinw. & Hornsch.) Jaeg.
intorquatum (Dozy & Molk.) Jaeg.
isocladum Dix. = *Hypnum plumaeforme* var. *minus*
kweichowense Bartr.
leptotapes (Card.) Sak.
monumentorum (Duby) Jaeg.
moritzii Jaeg.
nervosum Dix.
obtusulum (Card.) Iwats.
perminutum Broth. ex Bartr.
perreticulatum Broth. in Salm.
planulum Card. = *E. zollingeri*
shiragae Okam.
subplanulum Card. = *E. zollingeri* var. *zollingeri*
yasudae Broth.
zollingeri (C. Müll.) Jaeg. var. *zollingeri*
var. *formosicum* (Card.) Lai in Lai & Wang-Yang

Elmeriobryum Broth. (LEMBOPHYLLACEAE)
formosanum Broth. var. *formosanum*
var. *minus* Broth.
phillippinense Broth.

Encalypta Schreb. ex Hedw. (ENCALYPTACEAE)
alpina J. Sm.
breviseta C. Müll.
ciliata Hedw.
erythrodonta C. Müll.
giraldii C. Müll.
rhabdocarpa Schwaegr. var. *rhabdocarpa*
var. *spathulata* (C. Müll.) Husn.
spathulata C. Müll. = *E. rhabdocarpa* var. *spathulata*
tibetana Mitt.
vulgaris Hedw.

Endotrichella C. Müll. (PTEROBRYACEAE)
dietrichiae C. Müll.
eberhardtii Broth. & Par. in Par.
elegans (Dozy & Molk.) Fleisch. in Broth.
fauriei (Broth. & Par.) Broth. = *E. elegans*

Entodon C. Müll. (ENTODONTACEAE)
acutifolius R.-l. Hu
aeruginosus C. Müll.
amblyophyllus C. Müll. = *E. caliginosus*
attenuatus Mitt. = *E. sullivantii* var. *versicolor*
brevisetus (Hook. & Wils.) Lindb.
caliginosus (Mitt.) Jaeg.
challengeri (Par.) Card. = *E. compressus*
chloropus Ren. & Card.
cladorrhizans (Hedw.) C. Müll.
cochleatus Broth. = *E. luridus*
complanatulus C. Müll. in Fleisch. = *E. pulchellus*
compressus C. Müll. ex Mizush. var. *compressus*
var. *zikaiwiensis* (Par.) R.-l. Hu
conchophyllus Card.
concinnus (De Not.) Par.
curvatirameus Card.
delavayi Besch. = *E. macropodus*
divergens Broth.
dolichocucullatus Okam.
drummondii (Sull.) Jaeg. = *E. macropodus*
eurhynchioides Herz. & Nog. = *E. obtusatus*
excavatus Broth. = *E. macropodus*
flavescens (Hook.) Jaeg.
giraldii C. Müll.
griffithii (Mitt.) Jaeg. = *E. flavescens*
kungshanensis R.-l. Hu
latifolius Broth. = *E. prorepens*
longicostatus Buck = *E. sullivantii* var. *versicolor*
longifolius (C. Müll.) Jaeg.
luridus (Griffith) Jaeg.
macropodus (Hedw.) C. Müll.
mairei Thér. & Copp.
micropodus Besch.
microthecius Broth. = *E. compressus* var. *compressus*
morrisonensis Nog.
myurus (Hook.) Hampe var. *myurus* [Not included in China by Hu, 1983]
var. *hokinensis* Besch. [Not included in China by Hu, 1983]
nanocarpus C. Müll. var. nanocarpus = *E. compressus* var. *compressus*
var. zikaiwiensis (Par.) Gao = *E. compressus* var. *zikaiwiensis*
nepalensis Mizush. in Nog.
obtusatus Broth.
okamurae Broth. ex Card. = *E. luridus*
orthocarpus (Brid.) Lindb. = *E. concinnus*
perichaetialis (Card.) Nog. & Toyama = *E. brevisetus*

plicatus C. Müll.
prorepens (Mitt.) Jaeg.
pseudo-orthocarpus C. Müll. = *E. caliginosus*
pulchellus (Griffith) Jaeg.
pylaisioides R.-l. Hu & Y.-f. Wang
ramulosus Mitt. = *E. flavescens*
rubicundus (Mitt.) Jaeg. = *E. flavescens*
sakuraii Broth. = *E. perichaetialis*
scariosus Ren. & Card.
schensianus C. Müll.
seductrix (Hedw.) C. Müll. [Not included in As 2 by Buck, 1980]
serpentinus C. Müll. = *E. caliginosus*
smaragdinus Par. & Broth.
stenopyxis Thér. = *E. prorepens*
subramulosus Broth. = *E. caliginosus*
sullivantii (C. Müll.) Lindb. var. *sullivantii*
var. *versicolor* (Besch.) Mizush. in Wijk & Marg.
taiwanensis C.-k. Wang & S.-h. Lin
viridulus Card.
yunnanensis Thér. [Not included in China by Hu, 1983]
zikaiwiensis Par. = *E. compressus* var. *zikaiwiensis*

Entosthodon Schwaegr. (FUNARIACEAE)
buseanus Dozy & Molk. = *Funaria buseana*
physcomitrioides (Mont.) Mitt. = *Funaria physcomitrioides*

Ephemerum Hampe (EPHEMERACEAE)
apiculatum Chen
cohaerens (Hedw.) Hampe
serratum (Hedw.) Hampe

Epipterygium Lindb. (BRYACEAE)
tozeri (Grev.) Lindb.
wrightii (Sull.) Lindb.

Eriopus (Brid.) Brid. (HOOKERIACEAE)
cristatus (Hedw.) Brid.
japonicus Card. & Thér. = *Calyptrochaeta japonica*
parviretus Fleisch. = *Calyptrochaeta parviretus*
spinosus Nog.

Erpodium (Brid.) Brid. (ERPODIACEAE)
biseriatum (Aust.) Aust.

Erythrodontium Hampe (ENTODONTACEAE)
julaceum (Schwaegr.) Par.
leptothallium (C. Müll.) Nog. = *Eurohypnum leptothallum*
warmingii Hampe
sp. [as Gollania tereticaulis Broth. (Ando et al., 1957)]

Eucladium B.S.G. (POTTIACEAE)
verticillatum (Brid.) B.S.G.

Eumyurium Nog. (MYURIACEAE)
sinicum (Mitt.) Nog.
var. *flagelliferum* (Sak.) Nog.

Eurhynchium B.S.G. (BRACHYTHECIACEAE)
angustirete (Broth.) T. Kop. = *E. striatum*
arbuscula Broth. var. acuminatum Tak. = *Kindbergia arbuscula*
asperisetum (C. Müll.) Bartr.
celebicum (Lac.) Bartr.
coarctum C. Müll.
eustegium (Besch.) Dix.
hians (Hedw.) Lac.
laxirete Broth. in Card. = *Oxyrrhynchium laxirete*
muelleri (Jaeg.) Bartr.
polystichum Par. = *E. savatieri*
pulchellum (Hedw.) Jenn.
riparioides (Hedw.) Richards
savatieri Schimp. ex Besch.
serricuspis C. Müll.
stokesii (Turn.) B.S.G. ex Schimp. = *Kindbergia praelonga*
striatum (Hedw.) Schimp.

Eurohypnum Ando (HYPNACEAE)
leptothallum (C. Müll.) Ando f. *leptothallum*
var. *tereticaule* Gao & K.-c. Chang

Exodictyon Card. (LEUCOBRYACEAE)
blumii (C. Müll.) Fleisch.
sullivantii (Dozy & Molk.) Fleisch.

Fabronia Raddi (FABRONIACEAE)
anacamptodens Gao in Gao, G-c. Zhang & Cao
ciliaris (Brid.) Brid.
enervis Broth.
mariei Card. in Broth. (nom. nud.)
matsumurae Besch. var. *matsumurae*
var. *yunnanensis* Thér.
microspora Gao in Gao, G.-c. Zhang & Cao
papillidens Gao in Gao, G.-c. Zhang & Cao
patentissima C. Müll.
perpilosa Broth. = *Rhizofabronia perpilosa*
rostrata Broth.
schensiana C. Müll.
schmidii C. Müll.
secunda Mont.

Fauriella Besch. (THELIACEAE)
robustiuscula Broth.
tenerrima Broth.
tenuis (Mitt.) Card. in Broth.

Fissidens Hedw. (FISSIDENTACEAE)
acutus Jaeg. = *F. mangarevensis*
adelphinus Besch.
adianthoides Hedw.
anomalus Mont.
areolatus Griffith
beckettii Mitt.
bogoriensis Fleisch.
borealis Gao = *F. bryoides* var. *bryoides*
brevinervis Broth.
bryoides Hedw. ssp. *bryoides* var. *bryoides*
var. *esquirolii* (Thér.) Iwats. & T. Suz.
var. hedwigii Limpr. = *F. bryoides* var. *bryoides*
var. *lateralis* (Broth.) Iwats. & T. Suz.
var. *ramosissimus* (Thér.) Iwats. & T. Suz. (hom. illeg.)
var. *schmidii* (C. Müll.) R. Chopra & S. Kumar
ssp. *viridulus* (Sw.) Kindb.
capitulatus Nog.
ceylonensis Dozy & Molk.
crassipes Wils. ex B.S.G.
crenulatus Mitt. var. *crenulatus*
var. *elmeri* (Broth.) Iwats. & T. Suz.
cristatus Wils. ex Mitt.
diversifolius Mitt.
diversiretus Broth. = *F. grandifrons* var. *grandifrons*
esquirolii Thér. = *F. bryoides* var. *esquirolii*
formosanus Nog.
garberi Lesq. & James = *F. microcladus*
geminiflorus Dozy & Molk. var. *nagasakinus* (Besch.) Iwats.
gemmaceus Herz. & P. de la Varde = *F. protonemaecola*
geppii Fleisch.
giraldii Broth.

grandifrons Brid. var. *grandifrons*
var. planicaulis (Besch.) Nog. = *F. grandifrons*
guangdongensis Iwats. & Z.-h. Li
gymnogynus Besch.
hetero-limbatus Sak. = *F. tosaensis*
hollianus Dozy & Molk.
hyalianus Hook. & Wils.
incognitus Gang.
incrassatus Sull. & Lesq. = *F. zippelianus*
intromarginatulus Bartr.
involutus Wils. ex Mitt.
irrigatus Broth. = *F. plagiochiloides*
javanicus Dozy & Molk.
laxus Sull. & Lesq.
mangarevensis Mont.
microcladus Thwaites & Mitt.
micro-serratus Sak. = *F. obscurirete*
mittenii Par. = *F. laxus*
nobilis Griffith
obscurirete Broth. & Par. in Broth.
obscurus Mitt.
osmundoides Hedw.
papillosus Lac.
perdecurrens Besch.
perexiguus C. Müll.
plagiochiloides Besch.
protonemaecola Sak.
robinsonii Broth.
ryukyuensis Broth. = *F. bryoides* var. *ramosissimus*
saxatilis Tuz. & Nog. = *F. strictulus*
schmidii C. Müll. = *F. bryoides* var. *schmidii*
schwabei Nog.
splachnobryoides Broth. in Schumann. & Laut. f. *subbrachyneuron* (Thér. & P. de la Varde) Herz.
strictulus C. Müll.
subinteger Broth. = *F. plagiochiloides*
subsessilis Chen
subxiphioides Broth. = *E. strictulus*
sylvaticus Griffith = *F. taxifolius*
taelingensis Gao = (?) *F. osmundoides*
taxifolius Hedw.
tosaensis Broth.
wichurae Broth. & Fleisch.
xiphioides Fleisch. = (?) *F. zollingeri*
yakumontanus Nog. = *F. obscurus*
yamamotoi Sak. = *F. bryoides* var. *esquirolii*
yunnanensis Besch. = *F. grandifrons* var. *grandifrons*
zippelianus Dozy & Molk. in Zoll.
zollingeri Mont.

Fleischerobryum Loeske (BARTRAMIACEAE)
longicolle (Hampe) Loeske [May be *F. macrophyllum*, Lin, 1984]
macrophyllum Broth.

Floribundaria Fleisch. (METEORIACEAE)
armata Broth. = *F. setschwanica*
aurea (Mitt.) Broth. ssp. *aurea*
ssp. *nipponica* (Nog.) Nog.
chloronema (C. Müll.) Broth. = *F. sparsa* var. *sparsa*
chrysonema (C. Müll.) Broth. = *Barbella chrysonema*
floribunda (Dozy & Molk.) Fleisch.
hookeri Broth. = *F. sparsa*
horridula Broth. var. horridula = *Chrysocladium flammeum*
var. rufescens Broth. = (?) *Chrysocladium flammeum* ssp. *flammeum*
intermedia Thér. = *F. thuidioides*
nipponica Nog. = *F. aurea* ssp. *nipponica*
pseudo-floribunda Fleisch.
setschwanica Broth.
sparsa (Mitt.) Broth. var. *sparsa*
var. *pilifera* (Nog.) Nog.
thuidioides Fleisch.
torquata C.-k. Wang & S.-h. Lin
walkeri (Ren. & Card.) Broth.

Fontinalis Hedw. (FONTINALACEAE)
antipyretica Hedw. var. *antipyretica*
ssp. gothica (Card. & Arn.) Podp. = *F. antipyretica* var. *gracilis*
var. *gigantea* (Sull.) Sull.
var. *gracilis* (Lindb.) Schimp.
var. livonica (G. Roth & Bock) Mönk. in H. Möll. = *F. antipyretica* var. *gigantea*
gothica Card. & Arn. = *F. antipyretica* var. *gracilis*
hypnoides Hartm. var. *hypnoides*
var. *plicatus* (Card.) Gao
squamosa Hedw.

Forsstroemia Lindb. (CRYPHAEACEAE)
cordata Dix.
cryphaeoides Card.
cryphaeopsis Dix.
filiformis M.-x. Zhang in Wu, Lou & M.-z. Wang (nom. nud.)
kusnezovii Broth.
laisoides (C. Müll.) Nog.
mandschurica Broth.
neckeroides Broth.
recurvimarginata Nog. var. *recurvimarginata*
var. *filiformis* Nog. in Chen (nom. nud.)
schensiana Broth. in Lev.
sinensis (Besch.) Par. var. *sinensis*
var. *minor* (Broth.) Par.
trichomitria (Hedw.) Lindb.
tripinnata (Dix.) Nog. = *Porotrichum tripinnatum*

Funaria Hedw. (FUNARIACEAE)
attenuata (Dicks.) Lindb.
buseana (Dozy & Molk.) Broth.
calcarea Wahlenb.
connivens C. Müll.
dentata Crome = *F. calcarea*
gracilis (Hook. f. & Wils.) Broth.
hygrometrica Hedw. var. *hygrometrica*
var. *calvescens* (Schwaegr.) Mont.
japonica Broth.
lignicola Broth.
microstoma Bruch ex Schimp.
muehlenbergii Hedw. f. ex Lam. & DC.
pallescens (Jur.) Lindb. in Broth.
pilifera (Mitt.) Broth.
sinensis Dix. in C. Yang (nom. nud.)
submicrostoma C. Müll. = *F. microstoma*

Gammiella Broth. (SEMATOPHYLLACEAE)
pterogonioides (Griffith) Broth.

Garckea C. Müll. (DITRICHACEAE)
comosa (Dozy & Molk.) Wijk & Marg. = *G. flexuosa*
flexuosa (Griffith) Marg. & Nork.
phascoides C. Müll. = *G. flexuosa*

Garovaglia Endl. (PTEROBRYACEAE)
crassiuscula Card. = *Pterobryopsis crassiuscula*

plicata (Brid.) Bosch & Lac.
taiwanensis Nog.
Geheebia Schimp. (POTTIACEAE)
gigantea (Funck) Boul. = *Barbula gigantea*
Giraldiella C. Müll. (HYPNACEAE)
levieri C. Müll.
Girgensohnia (Lindb.) Kindb. = *Pleuroziopsis* (PLEUROZIOPSACEAE)
ruthenica (Weinm.) Kindb. = *Pleuroziopsis ruthenica*
Glossadelphus Fleisch. (SEMATOPHYLLACEAE)
alaris Broth. & Yas.
anomalus Thér.
attenuatus Broth.
falcatulus Broth.
lingulatus (Card.) Fleisch.
malacocladus (Card.) Broth. = *Ectropothecium zollingeri*
nitidus Thér.
planifrons (Broth. & Par.) Fleisch. = *Ectropothecium zollingeri*
zollingeri (C. Müll.) Fleisch = *Ectropothecium zollingeri*
Glyphomitrium Brid. (PTYCHOMITRIACEAE)
acuminatum Broth. var. *acuminatum*
var. *brevifolium* Broth.
calycinum (Mitt.) Card.
daviesii (With.) Brid.
formosanum Iwats. var. *formosanum*
var. *serratum* Iwats. in Iwats. & Sharp
grandirete Broth. = *G. minutissimum*
humillimum (Mitt.) Card.
hunanense Broth.
minutissimum (Okam.) Broth.
warburgii (Broth.) Card. var. *warburgii*
var. *yunnanense* Thér. & Henry
Glyphothecium Hampe (PTYCHOMNIACEAE)
sciuroides (Hook.) Hampe
Gollania Broth. (RHYTIDIACEAE)
arisanensis Sak.
clarescens (Mitt.) Broth.
coclearifolia Broth. ex Sak. = *Taxiphyllum alternans*
densepinnata Dix. = *G. turgens*
densifolia Dix. = *Taxiphyllum aomoriense*
eurhynchioides Broth.
horrida Broth.
isopterygioides (Broth. & Par.) Broth.
neckerella (C. Müll.) Broth. var. *neckerella*
var. *coreensis* (Card.) Broth.
philippinensis (Broth.) Nog.
robusta Broth.
ruginosa (Mitt.) Broth.
sinensis Broth. & Par.
subtereticaulis Broth. & Yas.
tereticaulis Broth. = *Erythrodontium* sp. [Ando et al., 1957]
turgens (C. Müll.) Ando
varians (Mitt.) Broth.
Grimmia Hedw. (GRIMMIACEAE)
affinis Hornsch.
alpestris (Web. & Mohr) Schleich. ex Nees var. alpestris = *G. donniana* var. *donniana*
var. holzingeri (Card. & Thér.) G. Jones in Grout = *G. donniana* var. *holzingeri*
alpicola Sw. ex Hedw. = *Schistidium agassizii*
anodon B.S.G.
apiculata Hornsch.
apocarpa Hedw. = *Schistidium apocarpum*
var. gracile Röhl. = *Schistidium apocarpum*
aspera C. Müll.
atrata Miel. ex Hornsch.
chenii S.-h. Lin
commutata Hüb. = *G. affinis*
cucullata Lou & Wu
decalvata Card.
decipiens (Schultz) Lindb. in Hartm.
dimorphula C. Müll.
donniana J. Sm. var. *donniana*
var. *holzingeri* (Card. & Thér.) Wijk & Marg.
elatior Bruch ex Bals. & De Not.
elongata G. Kaulf. in Sturm
filicaulis C. Müll. = *Schistidium apocarpum*
handelii Broth.
hartmanii Schimp.
himalayana Mitt. = *G. chenii*
incurva Schwaegr.
kansuana C. Müll.
kirienensis Gao
laevigata (Brid.) Brid.
liliputana C. Müll.
longicapusula Gao & Cao in Gao, G.-c. Zhang & Cao
mammosa Gao & Cao in Gao, G.-c. Zhang & Cao
micropyxis Broth.
montana B.S.G. = *G. donniana* var. *donniana*
obtusifolia Gao & Cao in Gao, G.-c. Zhang & Cao
ovalis (Hedw.) Lindb. = *G. affinis*
pilifera P. Beauv.
plagiopodia Hedw.
pulvinata (Hedw.) J. Sm.
sessitana De Not.
sinensi-anodon C. Müll.
sinensi-apocarpa C. Müll. = *Schistidium apocarpum*
subconferta Broth. = *Schistidium apocarpum*
subtergestina C. Müll.
tenax C. Müll.
tergestina Tomm. ex B.S.G.
torquata Hornsch. ex Grev.
unicolor Hook. in Grev.
Gymnostomiella Fleisch. (POTTIACEAE)
longinervis Broth.
vernicosa (Hook.) Fleisch. = *G. longinervis*
Gymnostomum Nees & Hornsch. (POTTIACEAE)
aeruginosum J. Sm.
angustifolium K. Saito = *Tuerckheimia angustifolia*
aurantiacum (Mitt.) Jaeg.
calcareum Nees & Hornsch.
laxirete (Broth.) Chen
recurvirostre Hedw. = *Hymenostylium recurvirostre*
subrigidulum (Broth.) Chen
Gyroweisia Schimp. (POTTIACEAE)
brevicaulis (C. Müll.) Broth.
tenuis (Hedw.) Schimp.
yuennanensis Broth.
Habrodon Schimp. (FABRONIACEAE)
leucotrichus (Mitt.) H. Perss. = *Iwatsukiella leucotricha*
perpusillus (De Not.) Lindb.
piliferus Card. = *Iwatsukiella leucotricha*

Handeliobryum Broth. (NECKERACEAE)
setschwanicum Broth. = *Sciaromiopsis brevifolia*
Haplocladium (C. Müll.) C. Müll. (THUIDIACEAE)
angustifolium (Hampe & C. Müll.) Broth. = *Bryohaplocladium angustifolium*
discolor (Par. & Broth.) Broth.
fauriei (Broth. & Par.) Watan. = *H. strictulum*
incurvum Broth.
larminatii (Broth. & Par.) Broth.
microphyllum (Hedw.) Broth. ssp. microphyllum = *Bryohaplocladium microphyllum*
ssp. capillatum (Mitt.) Reim. = *Bryohaplocladium microphyllum*
minutifolium Thér.
paraphylliferum Broth. = *Bryohaplocladium microphyllum*
strictulum (Card.) Reim.
Haplodontium Hampe = *Mielichhoferia* (BRYACEAE) [Shaw & Crum, 1984]
sp. [Koponen et al., 1983]
Haplohymenium Dozy & Molk. (THUIDIACEAE)
flagelliforme Sav.
formosanum Nog.
longinerve (Broth.) Broth.
microphyllum (Broth. & Par.) Broth. = *H. triste*
pseudo-triste (C. Müll.) Broth.
sieboldii (Dozy & Molk.) Dozy & Molk.
triste (Ces.) Kindb.
Hedwigia P. Beauv. (HEDWIGIACEAE)
albicans Lindb. = *H. ciliata*
ciliata (Hedw.) Ehrh. ex P. Beauv. var. *ciliata* f. *ciliata*
f. *leucophaea* (B.S.G.) G. Jones in Grout
var. *viridis* B.S.G.
Hedwigidium B.S.G. (HEDWIGIACEAE)
integrifolium (P. Beauv.) Dix. in C. Jens.
Helodium Warnst. (THUIDIACEAE)
blandowii (Web. & Mohr) Warnst.
paludosum (Aust.) Broth.
sachalinense (Lindb.) Broth.
Herpetineuron (C. Müll.) Card. (THUIDIACEAE)
toccoae (Sull. & Lesq.) Card.
Herzogiella Broth. (HYPNACEAE)
perrobusta (Broth. ex Card.) Iwats.
seligeri (Brid.) Iwats.
turfacea (Lindb.) Iwats.
Heterocladium B.S.G. (THUIDIACEAE)
angustifolium (Dix.) Watan.
papillosum (Lindb.) Lindb.
Heterophyllium (Schimp.) Kindb. in Fleisch. (SEMATOPHYLLACEAE)
foliolatum (Card.) Wijk & Marg.
haldanianum (Grev.) Fleisch. = *Callicladium haldanianum*
nemorosum (Brid.) Kindb.
Himantocladium (Mitt.) Fleisch. (NECKERACEAE)
cyclophyllum (C. Müll.) Fleisch.
elegantulum Nog.
formosicum Broth. & Yas.
loriforme (Bosch & Lac.) Fleisch.
plumula (Nees) Fleisch.
Holomitrium Brid. (DICRANACEAE)
cylindraceum (P. Beauv.) Wijk & Marg.
densifolium (Wils.) Wijk & Marg.
griffithianum Mitt. = *H. densifolium*
japonicum Card. = *H. densifolium*
perichaetiale (Hook.) Brid.
vaginatum (Hook.) Brid. = *H. cylindraceum*
Homalia Schimp. (NECKERACEAE)
arcuata Bosch & Lac.
fauriei Broth.
japonica Besch.
microdendron (Mont.) Jaeg. = *Homaliodendron microdendron*
obtusata Mitt.
subarcuata Broth.
trichomanoides (Hedw.) B.S.G.
Homaliadelphus Dix. & P. de la Varde (NECKERACEAE)
laevidendatus (Okam.) Iwats.
sharpii (Williams) Sharp var. *rotundatus* (Nog.) Iwats.
targionianus (Mitt.) Dix. & P. de la Varde var. *targionianus*
var. laevidentatus (Okam.) Nog. = *H. laevidentatus*
Homaliodendron Fleisch. (NECKERACEAE)
exiguum (Bosch & Lac.) Fleisch.
flabellatum (J. Sm.) Fleisch.
handelii Broth.
intermedium Herz.
javanicum (C. Müll.) Fleisch.
ligulaefolium (Mitt.) Fleisch.
microdendron (Mont.) Fleisch.
microphyllum Gao in Wu, Lou & M.-z.Wang (nom. nud.) = (?) *H. exiguum*
montagneanum (C. Müll.) Fleisch.
neckeroides Broth.
opacum Nog.
papillosum Broth.
pygmaeum Herz. & Nog.
rectifolium (Mitt.) Fleisch.
scalpellifolium (Mitt.) Fleisch. var. *scalpellifolium*
var. *angustifolium* Fleisch.
spathulaefolium (C. Müll.) Fleisch.
undulatum Nog.
Homalotheciella (Card.) Broth. (BRACHYTHECIACEAE)
sinensis Card. & Thér.
subcapillata (Hedw.) Broth.
Homalothecium B.S.G. (BRACHYTHECIACEAE)
laevisetum Lac.
leucodonticaule (C. Müll.) Broth.
longicuspis Broth.
nilgheriense (Mont.) Robins. = *Palamocladium nilgheriense*
nitens (Hedw.) Robins.
perimbricatum Broth. var. *perimbricatum*
var. *brevifolium* Tak.
philippeanum (Spruce) B.S.G.
sericeum (Hedw.) B.S.G.
sinense Par. & Broth.
tokiadense (Mitt.) Besch. = *H. laevisetum*
Homomallium (Schimp.) Loeske (HYPNACEAE)
connexum (Card.) Broth.
denticulatum Dix. = *H. connexum*
incurvatum (Brid.) Loeske
japonico-adnatum (Broth.) Broth.
leptothallum (C. Müll.) Nog. var. leptothallum = *Eurohypnum leptothallum*
plagiangium (C. Müll.) Broth.
yuennanense Broth.
Hondaella Dix. & Sak. (HYPNACEAE)

aulacophylla Dix. & Sak. = *H. brachytheciella*
brachytheciella (Broth. & Par.) Ando
Hookeria J. Sm. (HOOKERIACEAE)
acutifolia Hook. & Grev.
lucens (Hedw.) J. Sm.
nipponensis (Besch). Broth. = *H. acutifolia*
Hookeriopsis (Besch.) Jaeg. (HOOKERIACEAE)
geminidens Broth.
leiophylla (Besch.) Jaeg.
pappeana (Hampe) Jaeg.
utacamundiana (Mont.) Broth.
Horikawaea Nog. (PHYLLOGONIACEAE)
nitida Nog.
Hydrogonium (C. Müll.) Jaeg. (POTTIACEAE)
amplexifolium (Mitt.) Chen
anceps (Card.) Herz. & Nog.
arcuatum (Griffith) Wijk & Marg.
consanguineum (Thwaites & Mitt.) Hilp.
dixonianum Chen
ehrenbergii (Lor.) Jaeg.
gracilentum (Mitt.) Chen
javanicum (Dozy & Molk.) Hilp. var. *javanicum*
var. *convolutifolium* (Dix.) Chen
laevifolium (Broth. & Yas.) Chen
majusculum (C. Müll.) Chen
pseudo-ehrenbergii (Fleisch.) Chen
setschwanicum (Broth.) Chen
subcomosum (Broth.) Chen
subpellucidum (Mitt.) Hilp. var. *subpelludicum*
var. *hyaloloma* Herz.
williamsii Chen
Hygroamblystegium Loeske (AMBLYSTEGIACEAE)
fluviatile (Hedw.) Loeske ssp. noterophilum (Sull. & Lesq.) Grout = *Amblystegium noterophilum*
irriguum (Hook. & Wils.) Loeske = *Amblystegium tenax*
tenax (Hedw.) Jenn. = *Amblystegium tenax*
Hygrohypnum Lindb. (AMBLYSTEGIACEAE)
alpestre (Hedw.) Loeske
dilatatum (Wils.) Loeske
eugyrium (B.S.G.) Broth.
fontinaloides Chen
luridum (Hedw.) Jenn. var. *luridum*
var. *ehlei* (Arn.) Wijk & Marg.
var. *subsphaericarpum* (Brid.) C. Jens. in Podp.
molle (Hedw.) Loeske
montanum (Lindb.) Broth.
norvegicum (B.S.G.) Amann
ochraceum (Wils.) Loeske
palustre Loeske = *H. luridum* var. *luridum*
poecilophyllum Dix.
smithii (Sw.) Broth. var. *smithii*
var. *goulardii* (Schimp.) Wijk & Marg.
Hylocomiopsis Card. (THUIDIACEAE)
ovicarpa (Besch.) Card.
Hylocomium B.S.G. (HYLOCOMIACEAE)
alaskanum (Lesq. & James) Aust.
brevirostre (Brid.) B.S.G. var. *brevirostre*
var. *cavifolium* (Lac.) Nog.
cavifolium Lac. = *H. brevirostre* var. *cavifolium*
himalayanum (Mitt.) Jaeg.
proliferum (Brid.) Lindb. = *H. splendens*
pyrenaicum (Spruce) Lindb.
splendens (Hedw.) B.S.G.
umbratum (Hedw.) B.S.G.
yunnanense Besch. = *Neodolichomitra yunnanensis*
Hymenostomum R. Br. (POTTIACEAE)
edentulum (Mitt.) Besch.
exertum (Broth.) Broth. = *Weissia exserta*
latifolium Nog.
malayense Fleisch. = *Barbula cruegeri*
microstomum (Hedw.) R. Br. in Nees & Hornsch.
Hymenostyliella Bartr. (POTTIACEAE)
japonica (Broth.) K. Saito = *Didymodon japonicus*
Hymenostylium Brid. (POTTIACEAE)
aurantiacum Mitt. = *H. recurvirostre*
curvirostre Mitt. = *H. recurvirostre*
diversirete Broth. = *Reimersia inconspicua*
laxirete Broth. = *Gymnostomum laxirete*
recurvirostre (Hedw.) Dix.
Hyocomium B.S.G. (HYPNACEAE)
armoricum (Brid.) Wijk & Marg.
Hyophila Brid. (POTTIACEAE)
involuta (Hook.) Jaeg.
javanica (Nees & Blume) Brid.
propagulifera Broth.
setschwanica (Broth.) Hilp. ex Chen
spathulata (Harv.) Jaeg.
stenophylla Card. = *Trichostomum platyphyllum*
Hypnodendron (C. Müll.) Lindb. ex Mitt.(HYPNODENDRACEAE)
formosicum Card. = *H. vitiense*
reinwardtii (Reinw. & Hornsch.) Lindb. in Dozy & Molk.
vitiense Mitt. in Seem.
Hypnum Hedw. (HYPNACEAE)
alare (C. Müll.) Par. = *H. plumaeforme* var. *sinensi-molluscum*
arcuatum Lindb. = *H. lindbergii*
calcicolum Ando
callichroum Brid.
cupressiforme Hedw.
densirameum Ando
erectiusculum Sull. & Lesq.
fertile Sendtn.
filare (C. Müll.) Par. = *H. cupressiforme*
flaccens Besch. = *H. macrogynum*
hamulosum B.S.G.
homaliaceum (Besch.) Doign. = *H. erectiusculum*
kushakuense Card.
leptothallum (C. Müll.) Par. = *Eurohypnum leptothallum*
lindbergii Mitt.
macrogynum Besch.
minutum (C. Müll.) Par. = *H. plumaeforme* var. *sinensi-molluscum*
oldhamii (Mitt.) Jaeg.
pallescens (Hedw.) P. Beauv. var. *pallescens*
var. reptile (Michx.) Husn. = *H. pallescens* var. *pallescens*
plumaeforme Wils. var. *plumaeforme*
var. *alare* (Par.) Iis.
var. *gracile* Broth.
var. *minus* Broth. ex Iis.
var. *sinensi-molluscum* (C. Müll.) Ando
var. *strictifolium* Broth.
pratense (Rabenh.) W. Koch ex Hartm.
procerrimum Mol. = *Pseudostereodon procerrimum*

pseudorevolutum Reim. = *Stereodontopsis pseudorevoluta*
reptile Michx. = *H. pallescens* var. *pallescens*
revolutum (Mitt.) Lindb.
setschwanicum (Broth.) Ando
shensianum Ando
siuzewii (Broth.) Broth. = *Brotherella yokohamae*
subimponens Lesq. ssp. *subimponens*
ssp. *ulophyllum* (C. Müll.) Ando
submolluscum Besch.
thelidictyon Sull. & Lesq. = *Rhaphidostichum boschii* ssp. *thelidictyon*
tristo-viride (Broth.) Par.
turgens (C. Müll.) Par.
vaucheri Lesq.
zickendrahtii Ren. & Card. = *H. macrogynum*
Hypopterygium Brid. (HOOKERIACEAE)
aristatum Bosch & Lac.
ceylanicum Mitt. = *H. tenellum*
fauriei Besch.
flavo-limbatum C. Müll.
formosanum Nog.
japonicum Mitt.
sinicum Mitt. = *H. tenellum*
tenellum C. Müll.
tibetanum Mitt.
Indusiella Broth. & C. Müll. in Broth. (GRIMMIACEAE)
thian-schanica Broth. & C. Müll. in Broth.
Ishibaea Broth. & Okam. = *Lescuraea* (BRACHYTHECIACEAE)
julacea (Besch. & Card.) Toyama = *Lescuraea saxicola*
Isopterygiopsis Iwats. (PLAGIOTHECIACEAE)
muelleriana (Schimp.) Iwats.
Isopterygium Mitt. (HYPNACEAE)
albescens (Hook.) Jaeg.
applanatum Fleisch.
arquifolium (Bosch & Lac.) Jaeg. = *I. pohliaecarpum*
bancanum (Lac.) Jaeg.
courtoisii Broth. & Par.
cuspidifolium Card. = *Taxiphyllum cuspidifolium*
expallescens Lev. in Okam.
laxissimum Card.
lioui Thér. & P. de la Varde
micans (Sw.) Kindb. var. *fulvum* (Jaeg.) Par. ex Iwats.
minutifolium Card. & Thér. = *I. albescens*
minutirameum (C. Müll.) Jaeg.
muellerianum (Schimp.) Jaeg. = *Isopterygiopsis muelleriana*
perchlorosum Broth. ex Iis. = *I. pohliaecarpum*
piliferum (C. J. Hartm.) Loeske
pohliaecarpum (Sull. & Lesq.) Jaeg.
serrulatum Fleisch.
sinense Broth. & Par.
subalbidum (Sull. & Lesq.) Mitt. = *I. minutirameum*
tenerum (Sw.) Mitt.
textori (Lac.) Mitt. = *I. pohliaecarpum*
Isotheciopsis Broth. (LEMBOPHYLLACEAE)
comes (Griff.) Nog. = *Neobarbella comes*
Isothecium Brid. (LEMBOPHYLLACEAE)
myosuroides Brid.
myurum Brid.
subdiversiforme Broth. var. *subdiversiforme*
var. *filiforme* Nog.
var. *formosanum* Nog.
viviparum Lindb. = *I. myurum*
Iwatsukiella Buck & Crum (FABRONIACEAE)
leucotricha (Mitt.) Buck & Crum
Jaffueliobryum Thér. (GRIMMIACEAE)
marginatum Thér.
Juratzkaea Lor. (FABRONIACEAE)
seminervis (Schwaegr.) Lor.
sinensis Fleisch. ex Broth.
Kiaeria I. Hag. (DICRANACEAE)
blytii (B.S.G.) Broth.
falcata (Hedw.) I. Hag.
starkei (Web. & Mohr) I. Hag.
Kindbergia Ochyra (BRACHYTHECIACEAE)
arbuscula (Broth.) Ochyra var. *arbuscula*
var. *acuminata* (Tak.) Ochyra
praelonga (Hedw.) Ochyra
Leiodontium Broth. (HYPNACEAE)
gracile Broth.
robustum Broth.
Leptobryum (B.S.G.) Wils. (BRYACEAE)
lutescens (Limpr.) Mönk.
pyriforme (Hedw.) Wils.
Leptocladiella Fleisch. = *Leptohymenium* (HYLOCOMIACEAE)
psilura (Mitt.) Fleisch. = *Leptohymenium tenue*
Leptocladium Broth. (THUIDIACEAE)
sinense Broth.
Leptodictyum (Schimp.) Warnst. (AMBLYSTEGIACEAE)
kochii (B.S.G.) Warnst. = *Amblystegium trichopodium*
riparium (Hedw.) Warnst. = *Amblystegium riparium*
Leptodontium (C. Müll.) Hampe ex Lindb. (POTTIACEAE)
gracillimum Nog.
handelii Thér.
nakaii Okam.
pergemmascens Broth. = *Bryoerythrophyllum pergemmascens*
scaberrimum Broth.
subfilescens Broth. = *L. handelii*
taiwanense Nog.
viticulosoides (P. Beauv.) Wijk & Marg. var. *viticulosoides*
var. *subdenticulatum* (C. Müll.) Wijk & Marg.
warnstorfii Fleisch.
Leptohymenium Schwaegr. (HYLOCOMIACEAE)
brachystegium Besch.
hokinense Besch.
macroalare Herz. = *Macrothamnium psilurum*
tenue (Hook.) Schwaegr.
Leptopterigynandrum C. Müll. (THUIDIACEAE)
austro-alpinum C. Müll.
incurvatum Broth.
stricticaule Broth.
subintegrum (Mitt.) Broth.
tenellum Broth.
Lescuraea B.S.G. (LESKEACEAE)
incurvata (Hedw.) Lawt.
morrisonensis (Tak.) Nog. (comb. inval. basion. non cit.)
mutabilis (Brid.) Lindb. ex I. Hag.
saxicola (B.S.G.) Milde
Leskea Hedw. (LESKEACEAE)
arenicola Best
consanguinea (Mont.) Mitt.
polycarpa Ehrh. ex Hedw.
scabrinervis Broth. & Par.

subacuminata Nog.
subfiliramea Broth. & Par.
Leskeella (Limpr.) Loeske (LESKEACEAE)
nervosa (Brid.) Loeske
tectorum (Brid.) Hag.
Leucobryum Hampe (LEUCOBRYACEAE)
aduncum Dozy & Molk.
angustissimum Broth.
armatum Broth.
bowringii Mitt.
brevicaule Besch. = *L. neilgherrense*
canadidum (P. Beauv.) Wils. in Hook. f. var. *pentastichum* (Dozy & Molk.) Dix.
glaucum (Hedw.) Ångstr. in Fr.
japonicum (Besch.) Card. ex Broth. = *L. neilgherrense*
javense (Britt.) Mitt.
juniperoideum (Brid.) C. Müll.
neilgherrense C. Müll.
scaberulum Card. in Ren. & Card.
scabrum Lac.
scalare C. Müll. ex Fleisch.
textorii Besch. = *L. neilgherrense*
Leucodon Schwaegr. (LEUCODONTACEAE)
angustiretis Dix.
coreensis Card.
denticulatus Broth. in C. Müll. = *L. exaltatus*
esquirolii Thér.
exaltatus C. Müll.
flagelliformis C. Müll. = *L. pendulus*
giraldii C. Müll. = *L. exaltatus*
lasioides C. Müll. = *Forsstroemia laisoides*
latifolius Broth.
luteolus Dix.
luteus Besch.
mollis Dix.
morrisonensis Nog.
pendulus Lindb.
perdependes Okam. = *L. pendulus*
radicalis M.-x. Zhang in X.-j. Li & M.-x. Zhang
sciuroides (Hedw.) Schwaegr.
secundus (Harv.) Mitt.
sinensis Thér.
squarricuspis Broth. & Par. = *L. esquirolii*
subulatulus Broth.
subulatus Broth.
tibeticus M.-x. Zhang
Leucoloma Brid. (DICRANACEAE)
bifidum (Brid.) Brid.
molle (C. Müll.) Mitt.
Leucomium Mitt. (HYPNACEAE)
aneurodictyon (C. Müll.) Jaeg.
Leucophanes Brid. (LEUCOBRYACEAE)
candidum (Schwaegr.) Lindb.
octoblepharioides Brid.
Levierella C. Müll. (ENTODONTACEAE)
fabroniacea C. Müll.
Lindbergia Kindb. (LESKEACEAE)
brachyptera (Mitt.) Kindb. var. *brachyptera* var. *austinii* (Sull.) Grout
brevifolia (Gao) Gao in X.-j. Li (editor)
japonica Card.
magniretis (C. Müll.) Broth. var. *magniretis* var. *yunnanensis* Thér. & Copp.
ovata Gao in Gao, G.-c. Zhang & Cao (nom. illeg.)
sinensis (C. Müll.) Broth.
Loeskeobryum Fleisch. in Broth. = *Hylocomium* (HYLOCOMIACEAE)
brevirostre (Brid.) Fleisch. in Broth. = *Hylocomium brevirostre*
Lopidium Hook. f. & Wils. in Hook. f. (HOOKERIACEAE)
concinnum (Hook.) Wils. in Hook. f.
javanicum Hampe = *L. struthiopteris*
nazeense (Thér.) Broth.
struthiopteris (Brid.) Fleisch.
trichocladon (Bosch & Lac.) Fleisch.
Lyellia R. Br. (POLYTRICHACEAE)
crispa R. Br.
minor Xu & Xiong
platycarpa Card. & Thér.
Macrocoma (C. Müll.) Grout (ORTHOTRICHACEAE)
hymenostomum (Mont.) Grout = *M. tenue* ssp. *sullivantii*
tenue (Hook. & Grev.) Vitt ssp. *sullivantii* (C. Müll.) Vitt
Macromitrium Brid. (ORTHOTRICHACEAE)
angustifolium Dozy & Molk.
brachycladulum Broth. & Par. ex Broth. = *M. prolongatum*
brevituberculatum Dix.
chungkingense Chen
courtoisii Broth. & Par.
cylindrothecium Nog.
fasciculare Mitt.
ferriei Card. & Thér.
formosae Card.
fortunatii Thér. var. *fortunatii*
var. *nigrescens* Tix.
foxworthyi Broth.
gebaueri Broth.
giraldii C. Müll. = *M. japonicum*
goniostomum Broth.
gymnostomum Sull. & Lesq.
handelii Broth.
heterodictyon Dix.
holomitrioides Nog.
hymenostomum Mont. = (?) *Macrocoma tenue* ssp. *sullivantii*
incurvum (Lindb.) Mitt. = *M. japonicum*
involutifolium (Hook. & Grev.) Schwaegr.
japonicum Dozy & Molk.
makinoi (Broth.) Par. = *M. japonicum*
melanostomum Par. & Broth.
moorcroftii (Hook. & Grev.) Schwaegr.
neelgheriense C. Müll. = *M. sulcatum* var. *neelgheriense*
nepalense (Hook. & Grev.) Schwaegr.
okamurae Broth. = *Macrocoma tenue* ssp. *sullivantii*
perottetii C. Müll. = *Macrocoma tenue* ssp. *sullivantii*
prolongatum Mitt.
quercicola Broth. var. *quercicola*
var. *angustifolium* Broth.
reinwardtii Schwaegr.
rhacomitrioides Nog.
sinense Bartr.
sulcatum (Hook.) Brid. var. *neelgheriense* (C. Müll.) C. Müll.
sullivantii C. Müll. = *Macrocoma tenue* ssp. *sullivantii*
syntrichophyllum Thér. & P. de la Varde
taiheizanense Nog.

taiwanense Nog.
tuberculatum Dix.
uraiense Nog.
Macrothamnium Fleisch. (HYLOCOMIACEAE)
cuculatophyllum Gao & Aur
delicatulum Broth.
javense Fleisch.
macrocarpum (Reinw. & Hornsch.) Fleisch.
psilurum (Mitt.) Nog.
setschwanicum Broth. = *M. macrocarpum*
submacrocarpum (Ren. & Card.) Fleisch.
Mastopoma Card. (SEMATOPHYLLACEAE)
perundulatum (Dix.) Horik. & Ando
Meesia Hedw. (MEESIACEAE)
longiseta Hedw.
triquetra (L. ex Richt.) Ångstr. f. *triquetra*
f. *crassifolia* Kab.
uliginosa Hedw. var. *uliginosa*
var. *alpina* (Bruch) Hampe
Meiothecium Mitt. (SEMATOPHYLLACEAE)
angustirete Broth.
Merceya Schimp. = *Scopelophila* (POTTIACEAE)
gedeana (Lac.) Nog. = *Scopelophila cataractae*
ligulata (Spruce) Schimp. = *Scopelophila ligulata*
thermalis Fleisch. ex Broth. var. compacta Fleisch. = *Scopelophila ligulata*
Merceyopsis Broth. & Dix. (POTTIACEAE)
sikkimensis (C. Müll.) Broth. & Dix. = *Scopelophila cataractae*
Mesonodon Hampe (ENTODONTACEAE)
flavescens (Hook.) Buck
Meteoriella Okam. (METEORIACEAE)
soluta (Mitt.) Okam. f. *soluta*
f. *flagellata* Nog.
Meteoriopsis Fleisch. ex Broth. (METEORIACEAE)
ancistrodes (Ren. & Card.) Broth. = *M. reclinata* var. *ancistrodes*
formosana Nog. = *M. reclinata* var. *formosana*
reclinata (C. Müll.) Fleisch. ex Broth. var. reclinata
var. *ancistrodes* (Ren. & Card.) Nog.
var. *ceylonensis* Fleisch.
var. *formosana* (Nog.) Nog.
var. *subreclinata* Fleisch.
sinense (C. Müll.) Broth. = *M. reclinata* var. *ceylonensis*
squarrosa (Hook.) Fleisch. in Broth. var. *squarrosa*
var. *longicuspis* Nog.
var. *pilifera* Lou
undulata Horik. & Nog.
Meteorium (Brid.) Dozy & Molk. (METEORIACEAE)
acutirameum Thér. & Copp. = *M. buchananii* ssp. *buchananii*
buchananii (Brid.) Broth. ssp. *buchananii*
ssp. *helminthocladulum* (Card.) Nog.
helminthocladulum (Card.) Broth. = *M. buchananii* ssp. *helminthocladulum*
helminthocladum (C. Müll.) Fleisch. = *M. subpolytrichum*
horikawae Nog. = *M. subpolytrichum* ssp. *horikawae*
latiphyllum Lou
miquelianum (C. Müll.) Fleisch. ex Broth. ssp. *miquelianum*
ssp. *atrovariegatum* (Card. & Thér.) Nog.
papillarioides Nog.
piliferum Nog. = *M. subpolytrichum* ssp. *horikawae*
rigidum Broth. = *M. buchananii* ssp. *buchananii*
subpolytrichum (Besch.) Broth. ssp. *subpolytrichum*
ssp. *horikawae* (Nog.) Nog.
taiwanense Nog.
Metzlerella I. Hag. = *Atractylocarpus* (DICRANACEAE)
alpina (Mild.) I. Hag. = *Atractylocarpus alpinus*
sinensis Broth. = *Atractylocarpus sinensis*
Microcampylopus (C. Müll.) Fleisch. (DICRANACEAE)
longifolius Nog. f. *longifolius*
f. *densifolius* Nog.
Microctenidium Fleisch. (HYPNACEAE)
assimile Broth.
heterophyllum Thér.
leveilleanum (Dozy & Molk.) Fleisch.
Microdendron Broth. (POLYTRICHACEAE)
sinense Broth.
Microdus Schimp. in Besch. (DICRANACEAE)
austro-exiguus (C. Müll.) Par.
brasiliensis (Duby) Thér.
laxiretis Broth. (hom. illeg.)
pomiformis (Griffith) Besch. in Par. = *M. brasiliensis*
sinensis Herz.
Micromitrium Aust. (EPHEMERACEAE)
tenerum (B.S.G.) Crosby
Mielichhoferia Nees & Hornsch. (BRYACEAE)
mielichhoferi (Hook.) Wijk & Marg. var. *mielichhoferi*
var. *japonica* (Besch.) Wijk & Marg.
sinensis Dix.
Mitthyridium Robins. (CALYMPERACEAE)
fasciculatum (Hook. & Grev.) Robins.
flavum (C. Müll.) Robins.
undulatum (Dozy & Molk.) Robins. [Not included in China by Lin, 1984]
Miyabea Broth. (THUIDIACEAE)
fruticella (Mitt.) Broth.
rotundifolia Card.
Mniobryum Limpr. (BRYACEAE)
albicans (Wahlenb.) Limpr. = *Pohlia wahlenbergii*
ludwigii (Schwaegr.) Loeske
lutescens (Limpr.) Loeske = *Leptobryum lutescens*
pulchellum (Hedw.) Loeske = *Pohlia lescuriana*
tapintzense (Besch.) Broth.
wahlenbergii (Web. & Mohr) Jenn. = *Pohlia wahlenbergii*
Mnium Hedw. (MNIACEAE)
ambiguum H. Müll.
arbuscula C. Müll. = *Plagiomnium arbuscula*
areolosum X.-j. Li & Zang = *Plagiomnium arbuscula*
arisanense Sak. = *M. laevinerve*
cinclidioides Hüb. = *Pseudobryum cinclidioides*
cuspidatum Hedw. var. cuspidatum = *Plagiomnium cuspidatum*
var. subintegrum Chen ex X.-j. Li & Zang = *Plagiomnium acutum*
var. trichomanes (Mitt.) Chen ex X.-j. Li & Zang = *Plagiomnium acutum*
decurrens Schimp. ex Salm. = *Plagiomnium japonicum*
denticulosum Chen ex X.-j. Li & Zang = *Plagiomnium succulentum*
drummondii Bruch & Schimp. = *Plagiomnium drummondii*
excurrens Par. & Broth.= *Plagiomnium acutum*

flagellare Sull. & Lesq. = *Trachycystis flagellaris*
formosicum Card. = *Plagiomnium succulentum*
handelii Broth. = *Orthomnion handelii*
heterophyllum (Hook.) Schwaegr.
horikawae Nog. = *Rhizomnium horikawae*
hornum Hedw.
immarginatum Broth. = *Trachycystis ussuriensis*
integro-radiatum Dix. = *Plagiomnium succulentum*
integrum Bosch & Lac. = *Plagiomnium integrum*
japonicum Lindb.= *Plagiomnium japonicum*
laevinerve Card.
latilimbatum X.-j. Li & Zang = *Plagiomnium ellipticum*
leucolepioides Chen ex X.-j. Li & Zang = *Trachycystis ussuriensis*
longimucronatum X.-j. Li & Zang = *M. lycopodioides*
longispinum X.-j. Li & Zang = *M. lycopodioides*
luteolimbatum Broth. = *Plagiomnium succulentum*
lycopodioides Schwaegr.
magnirete (Lindb. & Arn.) Kindb. var. polymorphum X.-j. Li & Zang = *M. marginatum*
marginatum (With.) P. Beauv.
maximoviczii Lindb. var. maximoviczii = *Plagiomnium maximoviczii*
var. angustilimbatum Dix. = *Plagiomnium maximoviczii*
var. emarginatum Chen ex X.-j. Li & Zang = *Plagiomnium maximoviczii*
medium B.S.G. = *Plagiomnium medium*
microphyllum Dozy & Molk. = *Trachycystis microphylla*
nakanishikii Broth. = *Plagiomnium succulentum*
orthorrhynchum Brid. = *M. thomsonii*
parvulum Mitt. = *Rhizomnium parvulum*
pseudo-lycopodioides C. Müll. & Kindb. in Macoun = *M. lycopodioides*
rhynchophorum Hook. = *Plagiomnium rhynchophorum*
rostratum Schrad. f. rostratum = *Plagiomnium rostratum*
f. coriaceum (Griffith) Kab. = *Plagiomnium rhynchophorum*
f. laxirete Kab. = *Plagiomnium succulentum*
f. microovale (C. Müll.) Kab. = *Plagiomnium maximoviczii*
rugicum Laur. = *Plagiomnium ellipticum*
sichuanense X.-j. Li & Zang = *Plagiomnium arbusculum*
spinosum (Voit) Schwaegr.
spinulosum B.S.G.
stellare Reichd. ex Hedw.
striatulum Mitt. = *Rhizomnium striatulum*
subundulatum Dix. ex Kab. = *Plagiomnium maximoviczii*
succulentum Mitt. var. integrum Nog. = *Plagiomnium succulentum*
tezukae Sak. = *Plagiomnium tezukae*
thomsonii Schimp.
trichomanes Mitt. = *Plagiomnium acutum*
undulatum Weis ex Hedw. var. densirete Broth. = *Plagiomnium arbuscula*
vesicatum Besch. = *Plagiomnium vesicatum*
yunnanense Thér. = *Plagiomnium maximoviczii*

Molendoa Lindb. (POTTIACEAE)
hornschuchiana (Hook.) Lindb. ex Limpr. f. *hornschuchiana*
f. *barbuloides* Broth.
japonica Broth. = *Didymodon japonicus*
roylei (Mitt.) Broth.
sendtneriana (B.S.G.) Limpr. var. *sendtneriana*
var. *yunnanica* Györf. in Thér.
yuennanensis Broth. = *M. sendtneriana* var. *yunnanica*

Myurella B.S.G. (THELIACEAE)
brevicosta Lou & Wu
julacea (Schwaegr.) B.S.G.
sibirica (C. Müll.) Reim.
sinensi-julacea C. Müll. = *M. julacea*
tenerrima (Brid.) Lindb.

Myuriopsis Nog. = *Eumyurium* (MYURIACEAE)
sinica (Mitt.) Nog. f. sinica = *Eumyurium sinicum*

Myurium Schimp. (MYURIACEAE)
foxworthyi (Broth.) Broth. = *Oedicladium fragile*
fragile (Card.) Broth. = *Oedicladium fragile*
rufescens (Reinw. & Hornsch.) Fleisch. = *Oedicladium rufescens*
tortifolium Chen = *Oedicladium tortifolium*

Myuroclada Besch. (BRACHYTHECIACEAE)
concinna Besch. = *M. maximowiczii*
maximowiczii (Borsz.) Steere & Schof.

Nanomitrium Lindb. = *Micromitrium* (EPHEMERACEAE)
tenerum (B.S.G.) Lindb. = *Micromitrium tenerum*

Neacroporium Iwats. & Nog. (SEMATOPHYLLACEAE)
flagelliferum (Sak.) Iwats. & Nog.

Neckera Hedw. (NECKERACEAE)
brachyclada Besch.
brevicaulis Broth. ex Card. = *Neckeropsis obtusata*
complanata (Hedw.) Hüb.
coreana Card.
crenata Harv. ex Nog.
crenulata Harv. in Hook.
crispa Hedw.
decurrens Broth. var. *decurrens*
var. *rupicola* Broth.
fauriei Card.
flexiramea Card. var. *flexiramea*
var. *attenuata* Nog.
formosana Nog.
konoi Broth. ex Card.
morrisonensis Nog.
pennata Hedw.
perpinnata Card. & Thér.
polyclada C. Müll.
setschwanica Broth.
tosaensis Broth. = *Neckeropsis obtusata*
yezoana Besch. var. *yezoana*
var. *hayachinensis* (Card.) Nog.

Neckeradelphus Steere (NECKERACEAE)
menziesii (Hook.) Steere

Neckeropsis Reich. (NECKERACEAE)
calcicola Nog.
gracilenta (Bosch & Lac.) Fleisch.
lepineana (Mont.) Fleisch.
nitidula (Mitt.) Fleisch.
obtusata (Mont.) Fleish. in Broth.
sinensis Chen = *Homaliadelphus targionianus*
undulata (Hedw.) Reich.

Neobarbella Nog. (METEORIACEAE)

attenuata Nog.
comes (Griffith) Nog.
pilifera (Broth. & Yas.) Nog.
Neodolichomitra Nog. (RHYTIDIACEAE)
gigantea Nog.
robusta (Broth.) Nog.
yunnanensis (Besch.) T. Kop.
Neopogonatum Xu & Xiong (POLYTRICHACEAE)
tibeticum Xu & Xiong
Octoblepharum Hedw. (LEUCOBRYACEAE)
albidum Hedw.
Oedicladium Mitt. (MYURIACEAE)
doii (Sak.) Iwats.
foxworthyii Broth. = *O. fragile*
fragile Card.
rufescens (Reinw. & Hornsch.) Mitt.
tortifolium (Chen) Iwats.
Okamuraea Broth. (RHYTIDIACEAE)
brachydictyon (Card.) Nog.
hakoniensis (Mitt.) Broth. var. *hakoniensis* f. *hakoniensis*
f. *multiflagillifera* (Okam.) Nog.
var. *ussuriensis* (Broth.) Nog.
Oligotrichum Lam. & DC. (POLYTRICHACEAE)
aligerum Mitt.
aristatulum Broth.
armatum Broth.
crossidioides Chen & Wan ex Xu & Xiong
falcatum Steere
formosanum Nog. = *O. suzukii*
hercynicum (Hedw.) Lam. & DC.
obtusatum Broth.
semi-lamellatum (Hook. f.) Mitt. var. *semi-lamellatum*
var. *yuennanense* Broth. ex Chen (nom. nud.)
serratomarginatum Lou & Wu
suzukii (Broth.) Chuang
Oncophorus (Brid.) Brid. (DICRANACEAE)
crispifolius (Mitt.) Lindb. var. *crispifolius*
var. *brevipes* (Card.) Thér.
virens (Hedw.) Brid.
wahlenbergii Brid. var. *wahlenbergii*
var. *japonicus* Nog.
var. *longisetus* Nog.
Oreas Brid. (DICRANACEAE)
martiana (Hoppe & Hornsch.) Brid.
Oreoweisia (B.S.G.) De Not. (DICRANACEAE)
laxifolia (Hook. f.) Kindb.
serrulata (Funck) De Not. = *O. torquescens*
setschwanica Broth.
torquescens (Brid.) Wijk & Marg.
weisioides Broth.
Orthoamblystegium Dix. & Sak. (LESKEACEAE)
longinerve (Card.) Toyama
Orthodicranum (B.S.G.) Loeske (DICRANACEAE)
flagellare (Hedw.) Loeske = *Dicranum flagellare*
fragilifolium (Lindb.) Podp. = *Dicranum fragilifolium*
montanum (Hedw.) Loeske
scottianum (Turn.) G. Roth in Cas.-Gil. = *Dicranum scottianum*
strictum Broth.
Orthodontium Schwaegr. (BRYACEAE)
infractum Dozy & Molk.
Orthomnion Wils. (MNIACEAE)
bryoides (Griffith) Wijk & Marg.
dilatatum (Mitt.) Chen
handelii (Broth.) T. Kop.
loheri Broth.
nudum Bartr.
piliferum T. Kop.
yunnanense T. Kop., X.-j. Li & Zang
Orthomniopsis Broth. (MNIACEAE)
japonica Broth. = *Orthomnion dilatatum*
Orthostichopsis Broth. (MYURIACEAE)
tetragona (Hedw.) Broth.
Orthothecium B.S.G. (ENTODONTACEAE)
chryseum (Schwaegr.) B.S.G.
intricatum (Hartm.) B.S.G.
rufescens (Brid.) B.S.G.
strictum Lor.
Orthotrichum Hedw. (ORTHOTRICHACEAE)
affine Schrad. ex Brid.
anomalum Hedw.
callistomoides Broth.
consobrinum Card.
courtoisii Broth. & Par.
crispifolium Broth.
decurrens Thér. = *O. exiguum*
erubescens C. Müll.
exiguum Sull. in A. Gray
fortunatii Thér.
hookeri Wils. ex Mitt.
leiocarpum B.S.G. = *O. striatum*
leiolecythis C. Müll.
macounii Aust. ssp. *macounii*
ssp. *japonicum* Iwats.
macrosporum C. Müll.
microsporum C. Müll. in Lev.
obtusifolium Brid.
revolutum C. Müll.
ruspestre Schleich. ex Schwaegr.
scaberrimum Broth.
soridum Sull. & Lesq. in Aust.
speciosum Nees in Sturm
striatum Hedw.
szuchuanicum Chen
Osterwaldiella Fleisch. ex Broth. (PTEROBRYACEAE)
monostricta Fleisch. ex Broth.
Oxyrrhynchium (B.S.G.) Warnst. (BRACHYTHECIACEAE)
biforme Broth.
hians (Hedw.) Loeske = *Eurhynchium hians*
laxirete (Broth.) Broth.
polystictum (Par.) Broth. = *Eurhynchium savatieri*
praelongum (Hedw.) Warnst. var. praelongum = *Kindbergia praelonga*
var. stoeksii (Turn.) Podp. = *Kindbergia praelonga*
protractrum (C. Müll.) Broth.
savatieri (Besch.) Broth. = *Eurhynchium savatieri*
speciosum (Brid.) Warnst.
swartzii (Turn.) Warnst.
Oxystegus (Limpr.) Hilp. (POTTIACEAE)
cuspidatus (Dozy & Molk.) Chen
cylindricus (Brid.) Hilp. = *O. tenuirostris*
tenuirostris (Hook. & Tayl.) A. J. Sm. var. *tenuirostris* sensu lato
var. *stenocarpus* (Thér.) Zander
Palamocladium C. Müll. (BRACHYTHECIACEAE)
euchloron (C. Müll.) Wijk & Marg.

macrostegium (Sull. & Lesq.) Iwats. & Tak. in Tak., Iwats. & Nog. var. *macrostegium*
var. *excavatum* (Dix. & Sak.) Tak. & Iwats.
nilgheriense (Mont.) C. Müll. f. *nilgheriense*
f. *luzonense* (Broth.) Tak., Iwats. & Nog.
sciureum (Mitt.) Broth. in Par. = *P. macrostegium* var. *macrostegium*
Palisadula Toyama (SEMATOPHYLLACEAE)
chrysophylla (Card.) Toyama
katoi auch. non. (Broth.) Iwats. [Iwatsuki, 1979] = *Oedicladium rufescens*
Paludella Brid. (MEESIACEAE)
squarrosa (Hedw.) Brid.
Papillaria (C. Müll.) C. Müll. in Ångstr. (METEORIACEAE)
acuminata Nog. = *P. crocea*
chrysoclada (C. Müll.) Jaeg.
cordatifolia Lou
crocea (Hampe) Jaeg.
cusipidifera (Hook. f. & Wils.) Jaeg. = *P. crocea*
feae C. Müll. ex Fleisch.
flexicaulis (Wils.) Jaeg.
fuscescens (Hook.) Jaeg.
helminthocladula Card. = *Meteorium buchananii* ssp. *helminthocladulum*
nigrescens auct. non (Hedw.) Jaeg. [Noguchi, 1976] = *Meteorium papillarioides*
semitorta (C. Müll.) Jaeg.
Paraleucobryum (Limpr.) Loeske (DICRANACEAE)
enerve (Thed.) Loeske
fulvum (Hook.) Loeske in Podp. = *Dicranum fulvum*
longifolium (Hedw.) Loeske
Pelekium Mitt. (THUIDIACEAE)
bifarium (Bosch & Lac.) Fleisch.
velatum Mitt.
Penzigiella Fleisch. (PTEROBRYACEAE)
robusta Broth. = *Neodolichomitra yunnanensis*
Phascum Hedw. (POTTIACEAE)
cuspidatum Schreb. ex Hedw.
Philonotis Brid. (BARTRAMIACEAE)
appresifolia Dix.
falcata (Hook.) Mitt. var. *falcata*
var. *carinata* (Mitt.) Ochi
fontana (Hedw.) Brid. var. *fontana* f. *fontana*
f. *aristinervis* Mönk.
var. *seriata* (Mitt.) Kindb.
hastata (Duby) Wijk & Marg.
lancifolia Mitt.
longiseta (Michx.) Britt.
lutea Mitt. = *P. fontana* var. *fontana* f. *fontana*
marchica (Hedw.) Brid.
mollis (Dozy & Molk.) Mitt.
nitida Mitt. = *P. revoluta*
palustris Mitt. = *P. turneriana*
papillatomarginata Lou & Wu
plumulosa Card. & Thér. = *P. nitida*
revoluta Bosch & Lac.
savatieriana (Besch.) Broth. = *P. thwaitesii*
setschuanica (C. Müll.) Par. = *P. nitida*
socia Mitt. = *P. thwaitesii*
speciosa (Griffith) Mitt.
thwaitesii Mitt.
turneriana (Schwaegr.) Mitt. var. *turneriana*
var. *robusta* Bartr.
vitrea Herz. & Nog.
Physcomitrium (Brid.) Brid. (FUNARIACEAE)
acuminatum B.S.G. = *P. eurystomum*
courtoisii Par. & Broth.
eurystomum Sendtn.
immersum Sull. in A. Gray
japonicum (Hedw.) Mitt.
limbatulum Broth. & Par.
platyphylloides Par.
pyriforme (Hedw.) Hampe
repandum (Griffith) Mitt.
sinensis-sphaericum C. Müll.
sphaericum (C.F. Ludw.) Fürnr. in Hampe
spurio-acuminatum Dix. = *P. eurystomum*
subeurystomum Card. = *P. japonicum*
systylioides C. Müll. = *P. sphaericum*
Pilotrichopsis Besch. (CRYPHAEACEAE)
dentata (Mitt.) Besch. var. *dentata*
var. *hamulata* Nog.
robusta Chen
Pinnatella Fleisch. (NECKERACEAE)
makinoi (Broth.) Broth.
pusilla Nog.
robusta Nog.
taiwanensis Nog.
Pireella Card. (PTEROBRYACEAE)
formosana Broth.
Plagiobryum Lindb. (BRYACEAE)
demissum (Hook.) Lindb.
giraldii (C. Müll.) Par.
zierii (Hedw.) Lindb. var. *longicollum* C. Müll.
Plagiomnium T. Kop. (MNIACEAE)
acutum (Lindb.) T. Kop.
arbuscula (C. Müll.) T. Kop.
confertidens (Lindb. & H. Arnell) T. Kop.
cuspidatum (Hedw.) T. Kop.
drummondii (Bruch & Schimp.) T. Kop.
ellipticum (Brid.) T. Kop.
integro-radiatum (Dix.) Gao & K.-c. Chang = *P. succulentum*
integrum (Bosch & Lac.) T. Kop.
japonicum (Lindb.) T. Kop.
maximoviczii (Lindb.) T. Kop.
medium (B.S.G.) T. Kop.
rhynchophorum (Hook.) T. Kop.
rostratum (Schrad.) T. Kop.
ssp. vesicatum (Besch.) Nog. in Nog. & Iwats. = *P. vesicatum*
succulentum (Mitt.) T. Kop.
tezukae (Sak.) T. Kop.
trichomanes (Mitt.) T. Kop. = *P. acutum*
vesicatum (Besch.) T. Kop.
Plagiopus Brid. (BARTRAMIACEAE)
oederi (Brid.) Limpr. var. *oederi*
var. *alpinus* (Schwaegr.) Dalla Torre & Sarnth.
Plagiothecium B.S.G. (PLAGIOTHECIACEAE)
aomoriense Besch. = *Taxiphyllum aomoriense*
brevicuspis Broth. = *Taxiphyllum alternans*
cavifolium (Brid.) Iwats.
var. *fallax* (Card. & Thér.) Iwats.
curvifolium Schleiph. ex Limpr.
denticulatum (Hedw.) B.S.G.
euryphyllum (Card. & Thér.) Iwats. var. *euryphyllum*
var. *brevirameum* (Card.) Iwats.
formosicum Broth. & Yas. var. *formosicum*
var. *rectiapex* D.-k. Li

glossophylloides Broth.
handelii Broth.
laetum B.S.G.
laevigatum Schimp. ex Besch. = (?) *Entodon compressus*
longisetum Lindb. = *P. sylvaticum*
neckeroideum B.S.G. var. *neckeroideum*
var. *nittakayamae* (Toyama) Iwats.
var. *sikkimense* Ren. & Card.
nemorale (Mitt.) Jaeg.
obtusulum (Card.) Broth.
piliferum (Hartm.) B.S.G. = *Isopterygium piliferum*
pilosum Broth. & Yas. = *Taxiphyllum pilosum*
platyphyllum Mönk.
roseanum B.S.G. = *P. cavifolium*
rotundifolium D.-k. Li = (?) *P. cavifolium*
splendens Schimp. ex Card. var. splendens = *P. euryphyllum*
var. brevirameum Card. = *P. euryphyllum*
subulatum Broth.
succulentum (Wils.) Broth.
sylvaticum (Brid.) B.S.G. var. *sylvaticum*
var. *neglectum* (Mönk.) Koppe
turgescens Broth. = *Taxiphyllum alternans*
undulatum (Hedw.) B.S.G. = (?) *P. neckeroideum* var. *neckeroideum*

Platydictya Berk. (AMBLYSTEGIACEAE)
jungermannioides (Brid.) Crum
subtile (Hedw.) Crum

Platygyrium B.S.G. (HYPNACEAE)
repens (Brid.) B.S.G.

Platyhypnidium Fleisch. (BRACHYTHECIACEAE)
esquirolii (Card. & Thér.) Broth.
longirameum (C. Müll.) Fleisch.
micro-rusciforme (C. Müll.) Fleisch.
muelleri (Jaeg.) Fleisch. = *Eurhynchium muelleri*
patentifolium (C. Müll.) Fleisch.
patulifolium (Card. & Thér.) Broth.
platyphyllum (C. Müll.) Fleisch.
riparioides (Hedw.) Dix. = *Eurhynchium riparioides*
schottmulleri (Broth.) Fleisch. = *Eurhynchium riparioides*

Pleuridium Rabenh. (DITRICHACEAE)
acuminatum Lindb.
julaceum Besch.
subulatum (Hedw.) Rabenh.
tenue Mitt.

Pleurochaete Lindb. (POTTIACEAE)
squarrosa (Brid.) Lindb.

Pleuropus Griffith = *Palamocladium* (BRACHYTHECIACEAE)
euchloron (C. Müll.) Broth. = *Palamocladium euchloron*
fenestratus Griffith = *Palamocladium nilgheriense*
sciureus (Mitt.) Toyama = *Palamocladium macrostegium*

Pleuroweisia Limpr. ex Schlieph. (POTTIACEAE)
schliephackei Limpr.

Pleuroziopsis Kindb. ex Britt. (PLEUROZIOPSACEAE)
ruthenica (Weinm.) Kindb.

Pleurozium (Sull.) Mitt. (ENTODONTACEAE)
schreberi (Brid.) Mitt.

Pogonatum P. Beauv. (POLYTRICHACEAE)
akitense Besch. = *P. neesii*
aloides (Hedw.) P. Beauv.
capillare (Michx.) Brid.
cirratum (Sw.) Brid.
contortum (Brid.) Lesq.
crossidioides Chen ex Wu, Lou & M.-z. Wang (nom. nud.)
fastigiatum Mitt.
formosanum Horik.
grandifolium (Lindb.) Jaeg. = *P. japonicum*
gymnophyllum Mitt.
handelii Broth.
hetero-contortum Horik. = *P. spurio-cirratum*
hetero-proliferm Horik. = *P. nudiusculum*
iliangense Chen & Wan (nom. nud.)
inflexum (Lindb.) Lac.
japonicum Sull. & Lesq.
junghuhnianum (Dozy & Molk.) Dozy & Molk. = *P. neesii*
kweitschouense Broth.
longicollum Chen & Wan (nom. nud.)
macrocarpon Broth.
macrophyllum Dozy & Molk. = *P. microstomum*
manchuricum Horik. = *Polytrichum manchuricum*
microdendron (C. Müll.) Par. = *P. urnigerum*
microstomum (Schwaegr.) Brid. var. *microstomum*
var. *ciliatum* Xu & Xiong
minus Xu & Xiong
muticum Broth.
neesii (C. Müll.) Dozy
nudicaule (Wright) Par.
nudiusculum Mitt.
oligotrichoides Horik. = *P. nudiusculum*
otaruense Besch.
paucidens Besch. = *P. microstomum*
pergranulatum Chen
perichaetiale (Mont.) Jaeg.
polythamnium (C. Müll.) Par. = *P. urnigerum*
setchwanicum Broth. = *P. perichaetiale*
spinulosum Mitt. var. *spinulosum*
var. *serricalyx* Bartr.
spurio-cirratum Broth.
subfuscatum Broth.
submicrostomum Broth.
takao-montanum Horik.
thomsonii (Mitt.) Jaeg. var. *thomsonii*
var. *tibetanum* Chen
tortipes (Mitt.) Jaeg.
urnigerum (Hedw.) P. Beauv. var. *urnigerum*
var. *subintegrifolium* (Arn. & C. Jens.) H. Möll.
yunnanense Besch.

Pohlia Hedw. (BRYACEAE)
acuminata Hoppe & Hornsch.
atrothecium (C. Müll.) Broth.
camptotrachela (Ren. & Card.) Broth.
cavalieri (Thér.) Chen ex Wu, Lou & M.-z. Wang (comb. inval. basion. non cit.)
ciliifera Broth.
cruda (Hedw.) Lindb.
crudoides (Sull. & Lesq.) Broth. var. *crudoides*
var. *revolvens* (Card.) Ochi
drummondii (C. Müll.) Andr. in Grout
elongata Hedw.
flexuosa Hook.
graciliformis (Card. & Thér.) Chen (comb. inval. basion. non cit.)
gracillima (Card.) Horik. & Ochi

laticuspis (Broth.) Chen (comb. inval. basion. non cit.)
lescuriana (Sull.) Iis.
longicollis (Hedw.) Lindb.
ludwigii (Spreng. ex Schwaegr.) Broth.
minor Schleich. ex Schwaegr. var. *minor*
ssp. *acuminata* (Hoppe & Hornsch.) Wijk & Marg.
nemicaulon (C. Müll.) Broth.
nutans (Hedw.) Lindb.
oedoneura (C. Müll.) Broth.
orthocarpula (C. Müll.) Broth.
polymorpha Hoppe & Hornsch. = *P. minor* var. *minor*
proligera (Kindb.) Broth.
propagulifera Broth. ex Chen (nom. nud.)
pulchella (Hedw.) Lindb. = *P. lescuriana*
pygmaea (Broth.) Chen (comb. inval. basion. non cit.)
saprophila (C. Müll.) Broth.
sphagnicola (B.S.G.) Broth.
subcompactula (Par.) Wijk & Marg.
subflexuosa Broth.
timmioides Broth. ex Chen (nom. nud.)
wahlenbergii (Web. & Mohr) Andr. in Grout
yunnanensis (Besch.) Broth.

Polytrichastrum G. Sm. (POLYTRICHACEAE)
alpinum (Hedw.) G. Sm. var. *alpinum*
var. *brevifolium* (R. Br.) Brass.
var. *fragariformis* (Xu & Xiong) Redf. & Wu, comb. nov. *Polytrichum alpinum* Hedw. var. *fragariformis* Xu & Xiong, Acta Bot. Yunn. 6: 182. 1984.
var. *leptocarpum* (Broth.) Redf. & Wu, comb. nov. *Polytrichum alpinum* Hedw. var. *leptocarpum* Broth., Symb. Sin. 4: 136. 1929.
var. *secundifolium* (Broth.) Redf. & Wu, comb. nov. *Polytrichum alpinum* Hedw. var. *secundifolium* Broth., Symb. Sin. 4: 137. 1929.
formosum (Hedw.) G. Sm. var. *formosum*
var. *densifolium* (Mitt.) Iwats. & Nog.
longisetum (Brid.) G. Sm.
ohioense (Ren. & Card.) G. Sm.

Polytrichum Hedw. (POLYTRICHACEAE)
alpinum Hedw. = *Polytrichastrum alpinum* var. *alpinum*
var. brevifolium (R. Br.) C. Müll. = *Polytrichastrum alpinum* var. *brevifolium*
chingdingense Chen ex Wu, Lou & M.-z. Wang (nom. nud.)
commune Hedw. var. *commune*
var. *jensenii* (I. Hag.) Mönk. in Warnst.
var. *swartzii* (Hartm.) Nyh.
crassilamellatum Xu & Xiong
decipiens Limpr. = *Polytrichastrum ohioense*
densifolium Wils. ex Mitt.
formosum Hedw. = *Polytrichastrum formosum*
var. densifolium (Mitt.) Osada & Yano = *Polytrichastrum formosum* var. *densifolium*
gracile Dicks. in Menz. = *Polytrichastrum longisetum*
jensenii I. Hag. = *P. commune* var. *jensenii*
junghuhnianum Dozy & Molk. = *Pogonatum neesii*
juniperinum Willd. ex Hedw. var. *juniperinum*
var. *affine* (Funck) Brid.
var. gracilius Wahlenb. = *P. juniperinum* var. *affine*
var. *piliferoides* Xu & Xiong
longisetum Sw. ex Brid.
manchuricum (Horik.) Gao & K.-c. Chang
ohioense Ren. & Card. = *Polytrichastrum ohioense*
piliferum Schreb. ex Hedw.
sinense Card. & Thér.
sphaerothecium (Besch.) C. Müll.
strictum Menz. ex Brid. = *P. juniperinum* var. *affine*
subformosum Besch. var. *yunnanense* Thér. & Copp.
tibetanum Gao in Gao & K.-c. Chang
xanthopilum Wils. ex Mitt.

Porotrichodendron Fleisch. (LEMBOPHYLLACEAE)
mahahaicum (C. Müll.) Fleisch.

Porotrichum (Brid.) Hampe (NECKERACEAE)
fruticosum (Mitt.) Jaeg.
gracilescens Nog.
perplexans Dix.
tripinnatum Dix.

Pottia (Reichenb.) Ehrh. ex Fürnr. (POTTIACEAE)
intermedia (Turn.) Fürnr.
lanceolata (Hedw.) C. Müll.
latifolia (Schwaegr.) C. Müll. = *Stegonia latifolia*
splachnobryoides C. Müll.
truncata (Hedw.) B.S.G.

Powellia Mitt. (RACOPILACEAE)
acutifolia Broth.
australis (Hampe) Broth.
involutifolia Mitt.

Pringleella Card. (DITRICHACEAE)
pleuridioides Card.
sinensis Broth.

Prionidium Hilp. (POTTIACEAE)
eroso-denticulatum (C. Müll.) Chen = *Didymodon eroso-denticulatus*
setschwanicum (Broth.) Hilp. = *Didymodon eroso-denticulatus*

Pseudatrichum Reim. (POLYTRICHACEAE)
spinosissimum Reim.

Pseudisothecium Grout = *Isothecium* (LEMBOPHYLLACEAE)
myosuroides (Brid.) Grout = *Isothecium myosuroides*

Pseudobarbella Nog. (METEORIACEAE)
angustifolia Nog.
assimilis (Card.) Nog. = *P. attenuata*
attenuata (Thwaites & Mitt.) Nog.
brevicuspes (Broth.) Nog. = *P. attenuata*
concavifolia (Nog.) Nog. = *P. attenuata*
formosica (Broth.) Nog. = *Barbella compressiramea*
kiushiuensis (Broth.) Nog. = *P. attenuata*
laosiensis (Broth. & Par.) Nog.
laxifolia Nog.
levieri (Ren. & Card.) Nog.
mollissima (Broth.) Nog. = *P. laosiensis*
niitakayamensis Nog. = *Floribundaria setschwanica*
ochracea (Nog.) Nog. = *Chrysocladium flammeum* ssp. *ochraceum*
propagulifera Nog.
validiramosa Wu & Lou

Pseudobryum (Kindb.) T. Kop (MNIACEAE)
cinclidioides (Hüb.) T. Kop.
speciosum (Mitt.) T. Kop.

Pseudoleskea B.S.G. (LESKEACEAE)

denudata (Kindb.) Best = *P. radicosa*
incurvata (Hedw.) Loeske = *Lescuraea incurvata*
papillarioides C. Müll.
radicosa (Mitt.) Mac. & Kindb.
setschwanica Broth.
yuennanensis Broth.
Pseudoleskeella Kindb. (LESKEACEAE)
catenulata (Schrad.) Kindb.
tectorum (Brid.) Kindb. ex Broth. = *Leskeella tectorum*
Pseudoleskeopsis Broth. (LESKEACEAE)
decurvata (Mitt.) Broth. = *P. zippelii*
integrifolia Broth.
japonica (Sull. & Lesq.) Iwats. = *P. zippelii*
orbiculata (Mitt.) Broth. var. orbiculata = *P. zippelii*
var. laticuspis (Card.) Thér. = *P. zippelii*
serrulata Card. & Thér.
zippelii (Dozy & Molk.) Broth.
Pseudopleuropus Tak. (BRACHYTHECIACEAE)
morrisonensis Tak.
Pseudopohlia Williams (BRYACEAE)
bulbifera Williams
yunnenansis Herz.
Pseudoterobryum Broth. (PTEROBRYACEAE)
laticuspis Broth.
tenuicuspis Broth.
Pseudoracelopus Broth. (POLYTRICHACEAE)
philippinensis Broth.
Pseudoscleropodium (Limpr.) Fleisch. ex Broth. (ENTODONTACEAE)
levieri (C. Müll.) Broth.
purum (Hedw.) Fleisch. in Broth.
Pseudospiridentopsis (Broth.) Fleisch. (TRACHYPODACEAE)
horrida (Card.) Fleisch. f. *horrida*
f. *laxifolia* Nog.
Pseudostereodon (Broth.) Fleisch. (HYPNACEAE)
procerrimum (Mol.) Fleisch. in Broth.
Pseudosymblepharis Broth. (POTTIACEAE)
angustata (Mitt.) Chen
duriuscula (Mitt.) Chen
papillosula (Card. & Thér.) Broth. = *P. angustata*
subduriuscula (C. Müll.) Chen
Pterigynandrum Hedw. (ENTODONTACEAE)
filiforme Hedw.
sinense P. de la Varde
Pterobryon Hornsch. in Mart. (PTEROBRYACEAE)
arbuscula Mitt.
subarbuscula Broth. var. *subarbuscula*
var. *longissima* Nog.
Pterobryopsis Fleisch. (PTEROBRYACEAE)
acuminata (Hook.) Fleisch.
angustifolia Nog.
arcuata Nog.
crassicaulis (C. Müll.) Fleisch.
crassiuscula (Card.) Broth.
cucullatifolia Okam.
handelii Broth. = *P. acuminata*
morrisonicola Nog. = *P. acuminata*
orientalis (C. Müll.) Fleisch.
setschwanica Broth.
subcrassicaulis Broth.
yuennanensis Broth. = *P. orientalis*
Pterogonium Sw. (LEUCODONTACEAE)
gracile (Hedw.) J. Sm. var. *gracile*
var. *tsinlingense* Chen ex M.-x. Zhang
Ptilium De Not. (HYPNACEAE)
crista-castrensis (Hedw.) De Not.
Ptychomitrium Fürnr. (PTYCHOMITRIACEAE)
dentatum (Mitt.) Jaeg.
evanidinerve (Broth.) Broth. = *P. wilsonii*
faueri Besch.
formosicum Broth. & Yas.
linearifolium Reim. & Sak.
longisetum Reim. & Sak. = *P. polyphylloides*
mairei (Thér.) Broth.
polyphylloides (C. Müll.) Par.
sinense (Mitt.) Jaeg. var. *sinense*
var. *humile* Nog.
var. microcarpum (C. Müll.) Card. in Broth. = *P. sinense*
tortula (Harv.) Jaeg.
wilsonii Sull. & Lesq.
Pylaisia Schimp. (HYPNACEAE)
brotheri Besch. = *Pylaisiella brotheri*
curviramea Dix.
entodontea C. Müll. = *Bryosedwickia entodontea*
plangiangia C. Müll. = *Homomallium plangiangium*
robusta Broth & Par. in P. de la Varde = *Pylaisiella robusta*
Pylaisiadelpha Card. (SEMATOPHYLLACEAE)
himalayana S.-h. Lin
Pylaisiella Kindb. ex Grout (HYPNACEAE)
brotheri (Besch.) Iwats. & Nog.
extenta (Mitt.) Ando
falcata (B.S.G.) Ando var. *falcata*
var. recurvatula (Broth.) Ando = *P. extenta*
polyantha (Hedw.) Grout
robusta (Broth. & Par.) Gao & K.-c. Chang
schimperi Grout = *P. selwynii*
selwynii (Kindb.) Crum, Steere & Anderson
Pylaisiopsis (Broth.) Broth. (SEMATOPHYLLACEAE)
speciosa (Mitt.) Broth.
Racelopodopsis Thér. (POLYTRICHACEAE)
camusii Thér.
Racomitrium Brid. (GRIMMIACEAE)
aciculare (Hedw.) Brid.
albipiliferum Gao & Cao in Gao, G.-c. Zhang & Cao
angustifolium Broth.
anomodontoides Card.
aquaticum (P. Beauv.) Brid.
barbuloides Card. = *R. canescens* var. *epilosum*
brevisetum Lindb.
canescens (Hedw.) Brid. var. *canescens*
var. *epilosum* H. Müll. ex Milde
var. ericoides (Hedw.) Hampe = *R. ericoides*
var. *tortuloides* Pil.
carinatum Card.
crispulum (Hook. f. & Wils.) Dix.
cucullatulum Broth.
delavayi Broth. & Par.
dicarpum Broth.
ericoides (Hedw.) Brid.
fasciculare (Hedw.) Brid. var. *fasciculare*
var. *atroviride* Card.
var. *orientale* Card.
heterostichum (Hedw.) Brid. var. *heterostichum*
var. *brachypodium* (Besch.) Nog.
var. *diminutum* (Card.) Nog.
var. *obtusum* (Brid.) Delogne
var. *occidentale* Ren. & Card.

var. *ramulosum* (Lindb.) Corb.
var. *sudeticum* (Funck) E. Bauer
himalayanum (Mitt.) Jaeg. = *Grimmia chenii*
javanicum Dozy & Molk. in Zoll. var. javanicum = *R. crispulum*
var. *incanum* Broth.
lanuginosum (Hedw.) Brid.
microcarpum (Hedw.) Brid.
molle Card.
perpusillum Broth. ex Wu, Lou & M.-z. Wang (nom. nud.)
protensum (A. Br.) Hüb. = *R. aquaticum*
subsecundum (Hook. & Grev.) Mitt.
sudeticum (Funck) B.S.G. = *R. heterostichum* var. *sudeticum*
varium (Mitt.) Jaeg.
yakushimense Sak. = *R. fasciculare* var. *atroviride*
Racopilum P. Beauv. (RACOPILACEAE)
aristatum Mitt.
ferriei Thér.
formosicum Horik.
spectabile Reinw. & Hornsch.
Rauiella Reim. (THUIDIACEAE)
fujisana (Par.) Reim.
scita (P. Beauv.) Reim.
Regmatodon Brid. (LESKEACEAE)
declinatus (Hook.) Brid.
handlelii Broth.
longinervis Gao in Gao, G.-c. Zhang & Cao
orthostegius Mont.
schwabei Herz. = *R. declinatus*
serrulatus (Dozy & Molk.) Bosch & Lac.
Reimersia Chen (POTTIACEAE)
inconspicua (Griffith) Chen
Rhabdoweisia B.S.G. (DICRANACEAE)
crenulata (Mitt.) Jameson
crispata (With.) Lindb.
fugax (Hedw.) B.S.G. f. subdenticulata (Boul.) Demar. = *R. crispata*
laevidens Broth. = *R. crenulata*
sinensis Chen = *R. crispata*
striata (Schrad.) Lindb. var. subdenticulata (Boul.) I. Hag. = *R. crispata*
Rhachithecium Broth. ex Le Jol. (ORTHOTRICHACEAE)
perpusillum (Thwaites & Mitt.) Broth.
Rhamphidium Mitt. (POTTIACEAE)
crassicostatum X.-j. Li
dicranoides (C. Müll.) Par.
vaginatum Broth.
Rhaphidostichum Fleisch. (SEMATOPHYLLACEAE)
boschii (Dozy & Molk.) Seki ssp. *boschii*
ssp. *thelidictyon* (Sull. & Lesq.) Seki
bunodicarpum (C. Müll.) Fleisch.
macrostictum (Broth. & Par.) Broth.
piliferum (Broth.) Broth.
Rhizofabronia (Broth.) Fleisch. (FABRONIACEAE)
perpilosa (Broth.) Broth.
Rhizogonium Brid. (RHIZOGONIACEAE)
badakense Fleisch. = *R. longiflorum*
dozyanum Lac.
longiflorum (Mitt.) Jaeg.
spiniforme (Hedw.) Bruch in Krauss
Rhizomnium (Broth.) T. Kop. (MNIACEAE)
horikawae (Nog.) T. Kop.
magnifolium (Horik.) T. Kop.
minutulum (Besch.) T. Kop. = *R. parvulum*
parvulum (Mitt.) T. Kop.
striatulum (Mitt.) T. Kop.
tuomikoskii T. Kop.
Rhodobryum (Schimp.) Hampe (BRYACEAE)
giganteum (Schwaegr.) Par.
laxelimbatum (Ochi) Iwats. & T. Kop.
longicaudatum Zhang & X.-j. Li in X.-j. Li (editor) = *Bryum billardieri*
roseum (Hedw.) Limpr.
spathulatum (Hornsch.) Pócs in Biz & Pócs
Rhynchostegiella (B.S.G.) Limpr. (BRACHYTHECIACEAE)
curviseta (Brid.) Limpr.
laeviseta Broth.
leptoneura Dix. & Thér.
tenella (Dicks.) Limpr.
Rhynchostegium B.S.G. (BRACHYTHECIACEAE)
acicula (Broth.) Broth.
confertum (Dicks.) B.S.G.
dasyphyllum C. Müll. in Lev.
gracilescens Broth.
herbaceum (Mitt.) Jaeg.
inclinatum (Mitt.) Jaeg.
leptomitophyllum C. Müll.
murale (Hedw.) B.S.G.
obsoletinerve Broth.
ovalifolium Okam.
pallenticaule C. Müll.
pallidifolium (Mitt.) Jaeg.
plumosum Thér.
riparioides (Hedw.) Card. in Tourr. = *Eurhynchium riparioides*
rubro-carinatum Sak.
serpenticaule (C. Müll.) Broth. in Lev.
sinense (Broth. & Par.) Broth.
subspeciosum (C. Müll.) C. Müll.
vagans (Harv.) Jaeg.
Rhytidiadelphus (Limpr.) Warnst. (RHYTIDIACEAE)
loreus (Hedw.) Warnst.
squarrosus (Hedw.) Warnst.
subpinnatus (Lindb.) T. Kop.
triquetrus (Hedw.) Warnst.
yunnanensis (Besch.) Broth. = *Neodolichomitra yunnanensis*
Rhytidium (Sull.) Kindb. (RHYTIDIACEAE)
rugosum (Hedw.) Kindb.
Rozea Besch. (HYPNACEAE)
diversifolia Broth.
microcarpa Broth. f. *microcarpa*
f. *elongata* Buck & Crum
myura Herz.
pterogonioides (Harv.) Jaeg.
viridis Besch.
Saelania Lindb. (DITRICHACEAE)
glaucescens (Hedw.) Broth. in Bom. & Broth.
Sakuraia Broth. (ENTODONTACEAE)
conchophylla (Card.) Nog. = *Entodon conchophyllus*
Sanionia Loeske = *Drepanocladus* (AMBLYSTEGIACEAE)
uncinata (Hedw.) Loeske = *Drepanocladus uncinatus*
Sasaokaea Broth. (AMBLYSTEGIACEAE)
aomoriensis (Par.) Kanda
Scabridens Bartr. (LEUCODONTACEAE)
sinensis Bartr.
Schistidium Brid. (GRIMMIACEAE)

agassizii Sull. & Lesq. in Sull. [Not included in As 2 by Bremer, 1980]
alpicola (Hedw.) Limpr. var. alpicola = *S. agassizii* var. *rivulare* (Brid.) Limpr.
ambiguum Sull. = *S. apocarpum* var. *apocarpum*
apocarpum (Hedw.) B.S.G. var. *apocarpum*
var. gracile (Röhl.) B.S.G. = *S. apocarpum* var. *apocarpum*
gracile (Röhl.) Limpr. = *S. apocarpum* var. *apocarpum*
liliputanum (C. Müll.) Deg.
maritimum (Turn.) B.S.G. [Not included in As 2 by Bremer, 1980]
strictum (Turn.) Loeske
tibetanum Lou & Wu
Schistostega Mohr (SCHISTOSTEGACEAE)
osmundacea Mohr = *S. pennata*
pennata (Hedw.) Web. & Mohr
Schlotheimia Brid. (ORTHOTRICHACEAE)
charrieri Thér. & P. de la Varde
fauriei Card.
grevilleana Mitt.
japonica Besch. & Card.
latifolia Card. & Thér.
pungens Bartr.
purpurascens Par.
rugulosa Nog.
Schwetschkea C. Müll. (FABRONIACEAE)
brevipes (Broth. & Par.) Broth.
courtoisii Broth. & Par.
formosica Card.
gymostoma Thér.
incerta Thér.
laxa (Wils.) Jaeg.
matsumurae Besch.
schweinfurthii C. Müll.
sinica Broth. & Par.
sublaxa Broth. & Par.
Schwetschkeopsis Broth. (FABRONIACEAE)
denticulata (Sull.) Broth. = *S. fabronia*
fabronia (Schwaegr.) Broth.
formosana Nog.
japonica (Besch.) Broth. = *S. fabronia*
subulata Chen ex Wu, Lou & M.-z. Wang (nom. nud.)
Sciaromiopsis Broth. (AMBLYSTEGIACEAE)
brevifolia Broth.
sinensis (Broth.) Broth.
Scleropodium B.S.G. (BRACHYTHECIACEAE)
coreense Card.
illecebrum B.S.G. = *S. touretii*
touretii (Brid.) L. Koch
Scopelophila (Mitt.) Lindb. (POTTIACEAE)
cataractae (Mitt.) Broth.
ligulata (Spruce) Spruce
sikkimensis C. Müll. in Ren. & Card. = *S. cataractae*
Scorpidium (Schimp.) Lindb. (AMBLYSTEGIACEAE)
turgescens (T. Jens.) Loeske
Scouleria Hook. in Drumm. (GRIMMIACEAE)
pulcherrima Broth.
rschewinii Lindb. & Arn.
Seligeria B.S.G (SELIGERIACEAE)
pusilla (Hedw.) B.S.G.
Sematophyllum Mitt. (SEMATOPHYLLACEAE)
batanense Broth. = *Acroporium stramineum*
caespitosum (Hedw.) Mitt.
demissum (Wils.) Mitt.
henryi (Par. & Broth.) Broth.
japonicum (Broth.) Broth. = *S. subhumile* ssp. *japonicum*
phoeniceum (C. Müll.) Fleisch.
pulchellum (Card.) Broth.
robustulum (Card.) Broth.
subhumile (C. Müll.) Fleisch. ssp. *subhumile*
ssp. *japonicum* (Broth.) Seki
tristiculum (Mitt.) Fleisch.
Semibarbula Herz. ex Hilp. (POTTIACEAE)
orientalis (Web.) Wijk & Marg. = *Barbula indica*
Sharpiella Iwats. = *Herzogiella* (HYPNACEAE)
seligeri (Brid.) Iwats. = *Herzogiella seligeri*
spinulosa (Sull. & Lesq.) Iwats. = *Herzogiella perrobusta*
Solmsiella C. Müll. = *Erpodium* (ERPODIACEAE)
biseriata (Aust.) Steere = *Erpodium biseriatum*
Sphaerotheciella Fleisch. (CRYPHAEACEAE)
sphaerocarpa (Hook.) Fleisch.
Sphagnum L. (SPHAGNACEAE)
acutifolioides Warnst.
acutifolium Ehrh. ex Schrad. = *S. nemoreum*
amblyphyllum (Russ.) Warnst. = *S. recurvum* var. *amblyphyllum*
angustifolium (C. Jens. ex Russ.) C. Jens.
aongstroemii Hartm.
auriculatum Schimp. = *S. subsecundum* var. *auriculatum*
beccarii Hampe
borneoense Warnst. = *S. papillosum*
capillifolium (Ehrh.) Hedw. = *S. nemoreum*
compactum Lam. & DC. var. *compactum*
var. *imbricatum* Warnst.
contortum K. Schultz var. subsecundum Bayrh. = *S. subsecundum*
cuspidatulum C. Müll.
cuspidatum Ehrh. ex G. F. Hoffm.
cymbifolium (Ehrh.) Hedw. = *S. palustre*
dicladum Warnst.
falcatulum Besch.
fimbriatum Wils. in Hook.
fuscum (Schimp.) Klinggr.
girgensohnii Russ.
imbricatum Hornsch. ex Russ.
incertum Warnst. & Card.
inundatum Russ. var. inundatum = *S. subsecundum* var. *inundatum*
var. *perfibrosum* P. de la Varde
jensenii Lindb. f.
junghuhnianum Dozy & Molk. ssp. *junghuhnianum*
ssp. *pseudomolle* (Warnst.) H. Suz.
khasianum Mitt.
luzonense Warnst.
magellanicum Brid.
medium Limpr. = *S. magellanicum*
microporum Warnst. ex Card.
miyabeanum Warnst.
molluscum Bruch = *S. tenellum*
multifibrosum X.-j. Li & Zang in X.-j. Li
nemoreum Scop.
obtusiusculum Lindb. ex Warnst.
obtusum Warnst.
okamurae Warnst.
oligoporum Warnst. & Card. = *S. microporum*
ovatum Hampe in C. Müll.

pallens Warnst. & Card.
palustre L.
papillosum Lindb.
pauciporosum Warnst. = *S. beccarii*
platyphyllum (Lindb.) Warnst. = *S. subsecundum* ssp. *platyphyllum*
plumulosum (Röll) Bott.
pseudo-cymbifolium C. Müll. = *S. palustre*
quinquefarium (Lindb.) Warnst.
recurvum P. Beauv. var. *recurvum*
var. *amblyphyllum* (Russ.) Warnst.
riparium Ångstr.
robustum (Warnst.) Röll
russowii Warnst. = *S. robustum*
sericeum C. Müll.
squarrosum Crome in Hoppe
subacutifolium Schimp. in Warnst.
subbicolor Hampe
subsecundum Nees in Sturm spp. *subsecundum* var. *subsecundum*
var. *auriculatum* (Schimp.) Schlieph.
var. *inundatum* (Russ.) C. Jens.
var. luzonense (Warnst.) C. Jens. in Broth. = *S. luzonense*
var. *yuennanense* C. Jens. in Broth.
ssp. *platyphyllum* (Lindb.) Hérib.
tenellum Ehrh. ex G. F. Hoffm.
teres (Schimp.) Ångstr. in G. F. Hartm.
tosaense Warnst. in Nog.
Spiridens Nees (SPIRIDENTACEAE)
reinwardtii Nees
Splachnobryum C. Müll. (POTTIACEAE)
giganteum Broth.
obtusum (Brid.) C. Müll.
Splachnum Hedw. (SPLACHNACEAE)
ampullaceum Hedw. var. *ampullaceum*
var. *brevisetum* Gao
luteum Montin ex Hedw.
ovatum Dicks. ex Hedw. = *S. sphaericum*
rubrum Montin ex Hedw.
sphaericum Hedw.
vasculosum Hedw.
Stegonia Vent. (POTTIACEAE)
latifolia (Schwaegr.) Vent. ex Broth.
Stereodon Mitt. = *Hypnum* (HYPNACEAE)
setschwanicus Broth. = *Hypnum setschwanicum*
siuzewii Broth. = *Brotherella yokohamae*
Stereodontopsis Williams (HYPNACEAE)
pseudorevoluta (Reim.) Ando
setschwanica (Broth.) Ando = *Hypnum setschwanicum*
Stereophyllum Mitt. (PLAGIOTHECIACEAE)
anceps (Bosch & Lac.) Broth.
indicum (Bél.) Mitt.
ligulatum Jaeg.
setschwanicum Broth.
Stokesiella (Kindb.) Robins. = *Kindbergia* (BRACHYTHECIACEAE)
arbuscula (Broth.) Robins. = *Kindbergia arbuscula*
Streblotrichum P. Beauv. (POTTIACEAE)
convolutum (Hedw.) P. Beauv.
obtusifolium (Hilp.) Chen
propaguliferum X.-j. Li & M.-x. Zhang
Struckia C. Müll. (SEMATOPHYLLACEAE)
argentata (Mitt.) C. Müll.
Symblepharis Mont. (DICRANACEAE)
helicophylla Mont. = *S. vaginata*
oncophoroides Broth.
reinwardtii (Dozy & Molk.) Mitt.
sinensis C. Müll. var. *sinensis*
var. *minor* C. Müll.
vaginata (Hook.) Wijk & Marg.
Symphyodon Mont. (SYMPHYODONTACEAE)
perrottetii Mont.
weymouthioides Card. & Thér.
yuennanesis Broth.
Syrrhopodon Schwaegr. (CALYMPERACEAE)
ambiguus (Hook.) Spreng.
armatispinosus P.-j. Lin
borneenis (Hampe) Jaeg.
flammeo-nervis C. Müll.
gardneri (Hook.) Schwaegr.
japonicus (Besch.) Broth.
konoi Card.
larminatii Broth. & Par.
lonchophyllus Dix. = *S. japonicus*
semperi C. Müll.
tosaensis Card.
tsushimae Card. = *S. larminatii*
Taiwanobryum Nog. (PRIONODONTACEAE)
speciosum Nog.
Taxiphyllum Fleisch. (HYPNACEAE)
alternans (Card.) Iwats.
aomoriense (Besch.) Iwats.
autoicum Thér.
cuspidifolium (Card.) Iwats.
formosanum Herz. & Nog.
giraldii (C. Müll.) Fleisch. = *T. taxirameum*
inundatum Reim.
pilosum (Broth. & Yas.) Iwats.
splendescens (C. Müll.) Fleisch.
squamatulum (C. Müll.) Fleisch. = *T. cuspidifolium*
subarcuatum (Broth.) Iwats.
taiwanense Sak.
taxirameum (Mitt.) Fleisch.
Taxithelium Spruce ex Mitt. (SEMATOPHYLLACEAE)
batanense Bartr.
instratum (Brid.) Broth. in Ren. & Card.
nepalense (Schwaegr.) Broth.
parvulum (Broth. & Par.) Seki
Tayloria Hook. (SPLACHNACEAE)
acuminata Hornsch.
alpicola Broth.
delavayi (Besch.) Besch.
indica Mitt.
kwangsiensis Reim. = *T. indica*
lingulata (Dicks.) Lindb.
recurvi-marginata Nog.
sinensis C. Müll.
splachnoides (Schwaegr.) Hook.
subglabra (Griffith) Mitt. var. *subglabra*
var. *spinosa* Dix.
Tetracladium (Mitt.) Broth. = *Bryonoguchia* (THUIDIACEAE)
molkenboeri (Lac.) Broth. = *Helodium sachalinense*
osadae Sak. = *Helodium sachalinense*
Tetraphis Hedw. (TETRAPHIDACEAE)
geniculata Girg. ex Milde
pellucida Hedw.
Tetraplodon B.S.G. (SPLACHNACEAE)
angustatus (Hedw.) B.S.G. var. *angustatus*
var. *integerrimus* (Herz.) Gao

bryoides Lindb. = *T. mnioides*
mnioides (Hedw.) B.S.G. var. *mnioides*
var. *cavifolius* Schimp.
var. *longisetus* Gao in Wu, Lou & M.-z. Wang (nom. nud.)
urceolatus (Hedw.) B.S.G.
Thamnium B.S.G. = *Thamnobryum* (NECKERACEAE)
alopecurum (Hedw.) B.S.G. = *Thamnobryum alopecurum*
laevinerve Broth. = *Thamnobryum laevinerve*
sandei Besch. = *Thamnobryum sandei*
Thamnobryum Nieuwl. (NECKERACEAE)
alopecurum (Hedw.) Nieuwl. ex Gang.
incurvum (Nog.) Nog. & Iwats. in Iwats.
latifolium (Bosch & Lac.) Nieuwl. = *T. pandum*
lavinerve Broth. ex Chen (nom. nud.)
pandum (Hook. f. & Wils.) Stone & G. Scott
plicatulum (Lac.) Iwats.
sandei (Besch.) Iwats. var. *sandei*
var. *cymbifolium* (Card.) Nog. & Iwats. in Iwats.
tumidium (Nog.) Nog. & Iwats. in Iwats.
Theriotia Card. (BUXBAUMIACEAE)
lorifolia Card.
Thuidium B.S.G. (THUIDIACEAE)
assimile (Mitt.) Jaeg.
bipinnatulum Mitt. = *T. sparsifolium*
brachymenium Herz.
brevirameum Dix. = *T. submicropteris*
cymbifolium (Dozy & Molk.) Dozy & Molk. var. *cymbifolium*
var. japonicum (Lac.) Sak. = *T. cymbifolium* var. *cymbifolium*
delicatulum (Hedw.) Mitt. var. *delicatulum*
var. *radicans* (Kindb.) Crum, Steere & Anderson
fuscatum Besch.
glaucinoides Broth.
glaucinum (Mitt.) Bosch & Lac.
kanedae Sak.
lejeuneoides Nog.
lepidoziaceum Sak.
minutulum (Hedw.) B.S.G. [May not occur in As 2]
orientale Mitt. ex Dix. = *T. glaucinoides*
perpapillosum Watan. = *T. pygmaeum*
philibertii Limpr. = *T. delicatulum* var. *radicans*
pycnothallum (C. Müll.) Par.
pygmaeum B.S.G.
recognitum (Hedw.) Lindb.
rubiginosum Besch.
sparsifolium (Mitt.) Jaeg.
subglaucinum Card.
submicropteris Card.
substrictulum Dix.
talongense Besch.
tamariscellum (C. Müll.) Bosch & Lac.
tibetanum Salm.
venustulum Besch.
vestitissimum Besch.
Thyridium Mitt. = *Mitthyridium* (CALYMPERACEAE)
fasciculatum (Hook. & Grev.) Mitt. = *Mitthyridium fasciculatum*
flavum (C. Müll.) Fleisch. = *Mitthyridium flavum*
Thysanomitrion Schwaegr. = *Campylopus* (DICRANACEAE)
blumii (Dozy & Molk.) Card. = *Campylopus umbellatus*
nigrescens (Mitt.) P. de la Varde = *Campylopus richardii*
Timmia Hedw. (TIMMIACEAE)
megapolitana Hedw. ssp. *megapolitana*
var. *bavarica* (Hessl.) Brid.
norvegica Zett.
schensiana C. Müll. = *T. megapolitina* ssp. *megapolitina*
Timmiella (De Not.) Limpr. (POTTIACEAE)
anomala (B.S.G.) Limpr.
diminuta (C. Müll.) Chen
leptocarpa Broth. = *T. anomala*
Tomenthypnum Loeske (BRACHYTHECIACEAE)
nitens (Hedw.) Loeske = *Homalothecium nitens*
Tortella (Lindb.) Limpr. (POTTIACEAE)
fragilis (Hook. & Wils.) Limpr.
humilis (Hedw.) Jenn.
tortuosa (Hedw.) Limpr.
yuennanensis Broth. = *Pseudosymblepharis subduriuscula*
Tortula Hedw. (POTTIACEAE)
caninervis (Mitt.) Broth.
desertorum Broth.
inermis (Brid.) Mont.
longimucronata X.-j. Li
mucronifolia Schwaegr.
muralis Hedw. var. *muralis*
var. *aestiva* Brid. ex Hedw.
var. *obcordata* (Schimp.) Limpr.
nankomontana Nog.
obtusifolia (Schwaegr.) Math.
planifolia X.-j. Li
princeps De Not.
pugionata (C. Müll.) Broth.
reflexa Brid.
ruralis (Hedw.) Gaertn., Meyer & Schreb.
schmidii (C. Müll.) Broth.
sinensis (C. Müll.) Broth. ex Lev.
sublimbata (Mitt.) Broth.
subuluta Hedw.
tortuosa (Ehrh. ex. Hedw.) Limpr. = *Tortella tortuosa*
yuennanensis Chen
Trachycystis Lindb. (MNIACEAE)
flagellaris (Sull. & Lesq.) Lindb.
immarginata (Broth.) Laz. = *T. ussuriensis*
microphylla (Dozy & Molk.) Lindb.
ussuriensis (Maack & Regel) T. Kop.
Trachyloma Brid. (PTEROBRYACEAE)
indicum Mitt. var. *indicum*
var. *latifolium* Nog.
planifolium (Hedw.) Brid.
Trachyphyllum Gepp in Hiern (ENTODONTACEAE)
inflexum (Harv.) Gepp in Hiern
Trachypodopsis Fleisch. (TRACHYPODACEAE)
auriculata (Mitt.) Fleisch.
crispatula (Hook.) Fleisch. = *T. serrulata* var. *crispatula*
densifolia Broth. = *T. serrulata* var. *crispatula*
formosana Nog.
lancifolium Wu
serrulata (P. Beauv.) Fleisch.
var. *crispatula* (Hook.) Zant.
var. *guilbertii* (Thér. & P. de la Varde) Zant.
Trachypus Reinw. & Hornsch. (TRACHYPODACEAE)

bicolor Reinw. & Hornsch. var. *bicolor*
var. brevifolius Broth. = *T. bicolor* var. *hispidus*
var. *hispidus* (C. Müll.) Card.
var. *scindifolius* (Sak.) Wijk & Marg.
var. sinensis (C. Müll.) Broth. = *T. bicolor* var. *hispidus*
var. *viridulus* (Mitt.) Zant.
humilis Lindb.
longifolius Nog.
subbicolor C. Müll. ex Card. = *T. bicolor* var. *viridulus*
Trachythecium Fleisch. (HYPNACEAE)
micropyxis (Broth.) Bartr.
verrucosum (Jaeg.) Fleisch. var. *verrucosum*
var. *binervulum* Herz.
Trematodon Michx. (DICRANACEAE)
acutus C. Müll. = *T. longicollis*
ambiguus (Hedw.) Hornsch.
drepanellus Besch. = *T. longicollis*
longicollis Michx.
stricticalyx Dix.
tonkinensis Besch.
Trichodon Schimp. (DITRICHACEAE)
cylindricus (Hedw.) Schimp.
muricatus Herz.
Trichosteleum Mitt. (SEMATOPHYLLACEAE)
aculeatum Broth. & Par. = *Rhaphidostichum boscii* ssp. *thelidictyon*
boschii (Dozy & Molk.) Jaeg. = *Rhaphidostichum boscii* ssp. *thelidictyon*
fissum Mitt.
hamatum (Dozy & Molk.) Jaeg.
mammosum (C. Müll.) Jaeg.
parvulum Broth. & Par. = *Taxithelium parvulum*
Trichostomum Bruch in F. Müll. (POTTIACEAE)
angustatum (Mitt.) Fleisch. = *Pseudosymblepharis angustata*
aristatulum (Broth.) Hilp. ex Chen (hom. illeg.)
barbuloides (Broth.) Chen (hom. illeg.)
brachydontium Bruch in F. Müll.
cylindricum Hedw. var. cylindricum = *Oxystegus tenuirostris*
var. denticuspis Broth. = *Oxystegus cuspidatus*
involutum Broth. (hom. illeg.)
obtusifolium Broth. = *Streblotrichum obtusifolium*
parvulum Broth. = *Oxystegus cuspidatus*
platyphyllum (Broth. ex Iis.) Chen
Trismegistia (C. Müll.) Broth. (SEMATOPHYLLACEAE)
lancifolia (Harv.) Broth.
undulata Broth. & Yas.
Tristichella Dix. (SEMATOPHYLLACEAE)
glabrescens Iwats.
Tristichium C. Müll. (DITRICHACEAE)
lorentzii C. Müll.
sinense Broth.
Tuerckheimia Broth. (POTTIACEAE)
angustifolia (K. Saito) Zander
Ulota Mohr ex Brid. (ORTHOTRICHACEAE)
bellissima Besch.
crispa (Hedw.) Brid. var. *crispa*
var. *longifolia* (Dix. & Sak.) Iwats.
drummondii (Hook. & Grev.) Brid.
eurystoma Nog.
macrocarpa Broth.
morrisonensis Horik. & Nog.
Venturiella C. Müll. (ERPODIACEAE)
sinensis (Vent.) C. Müll. var. *sinensis*
var. *angusti-annulata* Griffin & Sharp
Vesicularia (C. Müll.) C. Müll. (HYPNACEAE)
apiculata Broth. = *V. ferriei*
chlorotica (Besch.) Broth.
ferriei (Card. & Thér.) Broth.
flaccida (Sull. & Lesq.) Iwats.
marginata Thér.
montagnei (Bél.) Broth.
reticulata (Dozy & Molk.) Broth.
sasaokae Okam.
shimadae Okam.
stillicidiorum Broth.
subchlorotica Broth.
tonkinensis (Besch.) Broth.
Voitia Hornsch. (SPLACHNACEAE)
nivalis Hornsch. var. *nivalis*
var. *stenocarpa* Par.
Warburgiella C. Müll. in Broth. (SEMATOPHYLLACEAE)
cupressinoides C. Müll. ex Broth.
Webera Hedw. = *Pohlia* (BRYACEAE)
acuminata (Hoppe & Hornsch.) Schimp. = *Pohlia minor* ssp. *acuminata*
ciliifera Broth. = *Pohlia ciliifera*
commutata Schimp. = *Pohlia drummondii*
cruda (Hedw.) Fürnr. = *Pohlia cruda*
elongata (Hedw.) Schwaegr. = *Pohlia elongata*
graciliformis Card. & Thér. = *Pohlia graciliformis*
laticuspis Broth. = *Pohlia laticuspis*
polymorpha (Hoppe & Hornsch.) Schimp. = *Pohlia minor*
pygmaea Broth. = *Pohlia pygmaea*
timmioides Broth. = *Pohlia timmioides*
Weisiopsis Broth. (POTTIACEAE)
anomala Broth. & Par.
hyophiloides Dix. & Thér.
Weissia Hedw. (POTTIACEAE)
breviseta (Thér.) Chen
controversa Hedw. var. *controversa*
var. *minutissima* (Par.) Wijk & Marg.
crispa (Hedw.) Mitt.
edentula Mitt. = *Hymenostomum edentulum*
exserta (Broth.) Chen
longidens Card.
microstoma (Hedw.) C. Müll. = *Hymenostomum microstomum*
planifolia Dix.
semipallida C. Müll.
Wijkia Crum (SEMATOPHYLLACEAE)
benguetensis (Broth.) Crum
deflexifolia (Ren. & Card.) Crum
extenuata (Brid.) Crum
hornschuchii (Dozy & Molk.) Crum
juliformis (Herz. & Dix. ex Dix.) Crum
semitortipilia (Fl.) S.-h. Lin (comb. inval. basion. inval.)
tanytricha (Mont.) Crum
Wilsoniella C. Müll. (DICRANACEAE)
decipiens (Mitt.) Alst. in Dix. var. *decipiens*
var. *acutifolia* (Dix.) Wijk & Marg.
karsteniana C. Müll.
Zygodon Hook. & Tayl. (ORTHOTRICHACEAE)
brevisetus Wils. ex Mitt.
conoideus (Dicks.) Hook. & Tayl.

obtusifolius Hook.
reinwardtii (Hornsch.) A. Br. in B.S.G.
viridissimus (Dicks.) Brid.
yuennanensis Malta

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NOTES

A REMARKABLE NEW *SELAGINELLA* FROM VENEZUELA

Despite a recent treatment of South American spike mosses (Alston et al., 1981) in which 133 species are recognized, *Selaginella* in the Neotropics remains taxonomically difficult, with many undescribed species. In Venezuela alone, 74 species are now known, and many more will eventually be recorded. We describe one new one here, perhaps the largest known *Selaginella* in terms of girth and certainly the most robust American species.

Selaginella gigantea grows in colonies of several hundred plants in wet evergreen primary forest in the Coastal Cordillera of Venezuela. The particular site is in the Borburata Mountains of Estado Carabobo, a well-known refugium for many endemic taxa of vascular plants (Steyermark, 1979, 1982).

Selaginella gigantea Steyermark & A. R. Smith, sp. nov. TYPE: Venezuela. Carabobo: entre Los Tanques y La Toma, a lo largo del Río San Gián, al sur de Borburata, arriba de la Planta Electrica, 750 m, 1 Apr. 1966, *Steyermark & Steyermark 95418* (holotype, US 2549293; isotype, VEN). PARATYPES: same locality, 27 Mar. 1966, *Steyermark & Steyermark 95148* (G, VEN); 7 km S of Borburata, 10°23′30″N, 67°58′30″W, 16 Dec. 1983, *Steyermark, Berry & Manara 129691* (UC, VEN). Figures 1, 2.

Planta 1–2 metralis, caulibus erectis robustis articulatis 10–15 mm diam. glabris, parte inferiore 0.5 m rhizophora elongata ferenti; internodiis usque 10 mm diam. efoliatis vel foliis dissitis patentibus ovatis acutis integerrimis 3–4 × 1.75 mm; parte frondosa ambitu late ovato-lanceolata 4–5-pinnata ca. 70 × 30 cm, ramulis inferioribus 9–15 cm dissitis; ramis principalibus caulium ovatis vel oblongo-ovatis 7–14 × 3.5–7 cm in 15–30 divisiones secundarias lineares; foliis lateralibus divisionum secundariarum horizontaliter patentibus 13–29 paribus plerumque 4–5 × 1.25–1.5 mm lineari-subfalcatis oblique insertis apice acutis per totam latitudinem decurrentibus, marginibus integerrimis vel apicem versus remote serrulatis utrinque glabris; foliis axillaribus ellipticis acutis 3.5 × 1.5 mm integerrimis exauriculatis; foliis intermediis 1–1.7 × 0.2–0.5 mm acutis basi paullo asymmetricis exauriculatis per latitudinem adnatis; strobilis usque 20 × 1.5–2 mm in apicibus ramulorum singulatim dispositis; megasporophyllis basi strobili solitariis; microsporophyllis numerosis late deltoideis vel subrotundatis apice acuminatis vel breviter aristatis ca. 1.25 × 1.25 mm; megasporis cremeis ca. 1.2 mm diam. grosse rugosis; microsporis ca. 30 μm longis dense papillatis, prominentiis leviter capitatis.

Plant 1–2 m tall, erect, with many strongly ascending branches arising from the lower 0.5 m of main stem; stem and main branches stout, firm, with swollen, bronze-colored nodes 10–15 mm diam., glabrous; nodes 10–15 cm apart toward base of plant, drying brown and contracted, sending out aerial roots (rhizophores) to 6.5 mm diam. at the lower nodes; internodes to ca. 10 mm diam., stramineous, lacking leaves or leaves very remote, spreading, 3–4 mm by 1.75 mm, ovate, decurrent, acute, entire; stele T-shaped or X-shaped in cross section, with arms 2–3 mm long; frondose branch system broadly ovate-lanceolate in outline, 4–5 times divided with penultimate divisions pinnately arranged, each of the penultimate divisions 7–14 cm by 3.5–7 cm with 15–30 secondary linear divisions; lateral leaves of the secondary divisions 13–29 pairs horizontally spreading, linear-subfalcate, obliquely inserted, acute at apex, 4–5 mm by 1.25–1.5 mm, decurrent and attached along their width, contiguous or slightly imbricate at the base, but spatially separated for most of their length (at least in the dried state), entire or remotely serrulate along acroscopic margin, linear-subfalcate and narrowly acute at apex, glabrous on both sides and along margins; axillary leaves ca. 1.5 mm, elliptic, acute, entire, exauriculate; median leaves 1–1.7 mm by 0.2–0.5 mm, acute, glabrous, slightly asymmetric at base, exauriculate, adnate their width; strobili to 20 mm by 1.5–2 mm, solitary on the apices of penultimate branches, maturing simultaneously; megasporophylls single at base of strobilus, ca. 2 mm by 2–2.5 mm, broadly ovate to subrotund, rounded to subacute at tip; microsporophylls numerous, ca. 1.25 mm by 1.25 mm, broadly deltoid to subrotund, acuminate or short-aristate at apex; megaspores cream-colored, ca. 1.2 mm diam., coarsely rugose, 1–4 per sporophyll; microspores beige, ca. 30 μm long, densely papillate with blunt, slightly capitate projections, shed singly. Figures 3, 4.

The Steyermark, Berry and Manara collection, cited with coordinate details, was collected from

TABLE 1. Differences between *Selaginella exaltata* and *S. gigantea.*

Selaginella exaltata	*Selaginella gigantea*
Stem mainly clambering, sprawling, scandent, or reclining	Stem erect
Stem, in some portion, pubescent	Stem completely glabrous
Lateral leaves 3–4 mm long	Lateral leaves 4–5 mm long
Lateral leaves (in dried state at least) contiguous	Lateral leaves (dried state at least) well separated
Lateral leaves with short and narrowly decurrent bases	Lateral leaves with long and broadly decurrent bases
Axillary leaves auriculate	Axillary leaves exauriculate
Median leaves of ultimate and penultimate branch-systems 0.5–1 mm wide, narrowly white-margined, and more rounded on the outer edge	Median leaves 0.2–0.5 mm wide, not white-margined, and less curved on the outer edge
Lateral branches non-articulate or occasionally weakly articulate	Lateral branches decidedly articulate
Stele basically 3-lobed or T-shaped with xylem in several patches, each patch surrounded by phloem	Stele (at least in the main axes) with xylem in a solid strand, either X-shaped or T-shaped (see Mickel & Hellwig, 1969).
Penultimate branch-systems lanceolate, 7–17 cm by 1.5–5 cm, 3–4 times longer than broad	Penultimate branch-systems ovate or oblong-ovate, 7–14 cm by 3.5–7 cm, 1.5–2 times longer than broad
Penultimate branch-systems with 30–50 divisions	Penultimate branch-systems with 15–30 divisions

the type locality. Specimens have also been collected from the type locality by Aristeguieta and by Tamayo, but are not presently available.

This very distinctive and apparently taxonomically isolated species is perhaps most closely related to *S. exaltata* (Kunze) Spring, which is known from Costa Rica to Peru and western Brazil (Alston et al., 1981). That species differs in many respects from *S. gigantea.* These differences are presented in Table 1 (also see Figs. 1–4).

Somers (1978), in an unpublished thesis on the articulate Selaginellas (subg. *Stachygynandrum* ser. *Articulatae*), considered *Steyermark 95418* (the type) to represent a new species or possibly be of hybrid origin between *S. exaltata* and a nonarticulate taxon. The argument for hybrid origin was based partly on an examination of spores (sample of two), which Somers found to be hollow, and partly on evidence from sporangial dehiscence. According to Somers (1978, 1982), *S. exaltata* and other articulate species have a unique and more complex sporangial dehiscence. However, *S. gigantea* has the simpler bivalvate condition characteristic of the nonarticulate species. We confirm the bivalvate nature in *S. gigantea.* This casts some doubt on the affinities of *S. gigantea,* especially since it appears to have most of the other characteristics of the articulate species: single enlarged basal megasporangia, very large megaspores, beige microspores, and rhizophores orignating dorsally (Somers, 1982).

Even if the hybridization hypothesis could be shown to be true, the event most likely was ancient and the characteristics of *S. gigantea* now so distinctive that we believe it warrants description. Hybrid origin is difficult to invoke for yet another reason: *S. exaltata,* a most distinctive species itself and not likely to be overlooked by collectors, has never been found in Venezuela or the Guianas.

FIGURE 1. Paratype of *Selaginella gigantea* (*Steyermark, Berry & Manara 129691*), showing a portion of the lower stem with an elongated rhizophore.

FIGURE 2. Paratype of *Selaginella gigantea* (*Steyermark, Berry & Manara 129691*), showing an upper frondose branch.

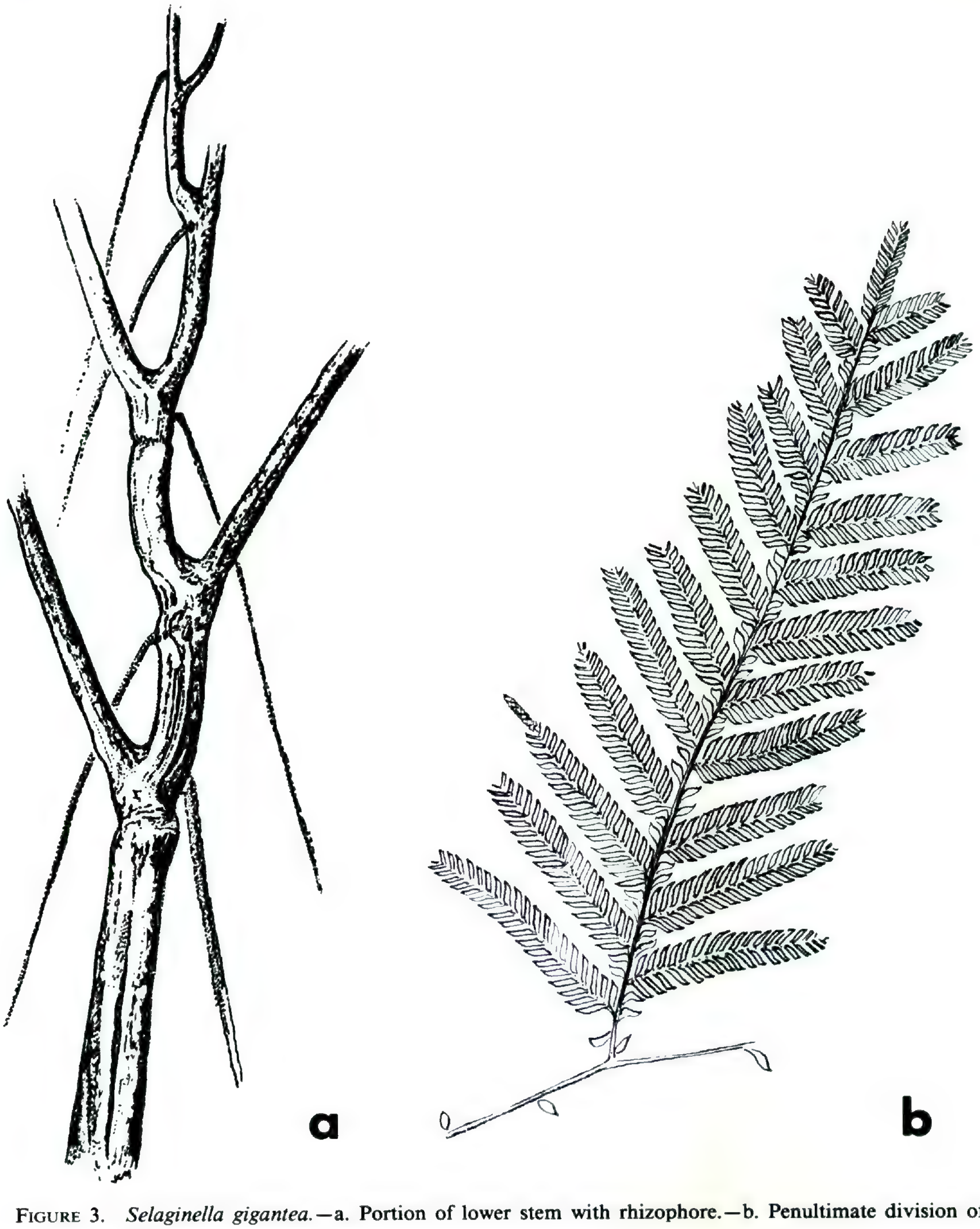
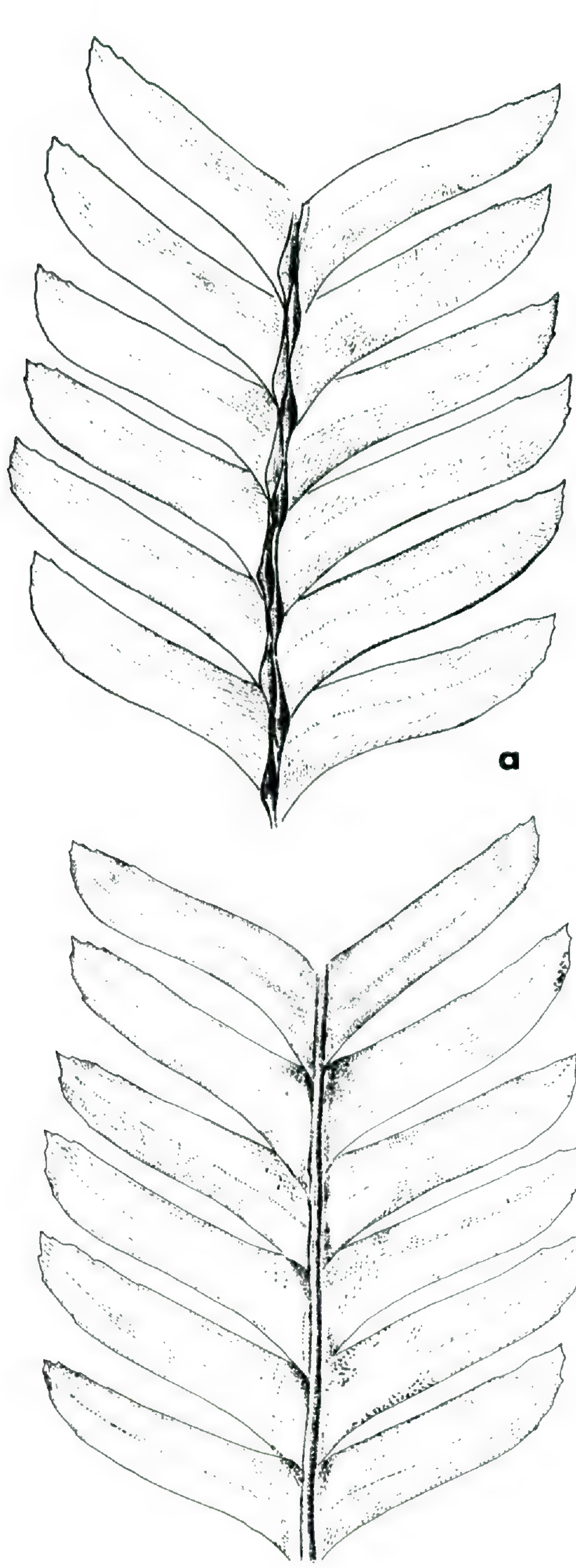


FIGURE 3. *Selaginella gigantea.*—a. Portion of lower stem with rhizophore.—b. Penultimate division of branch-system. ×1.



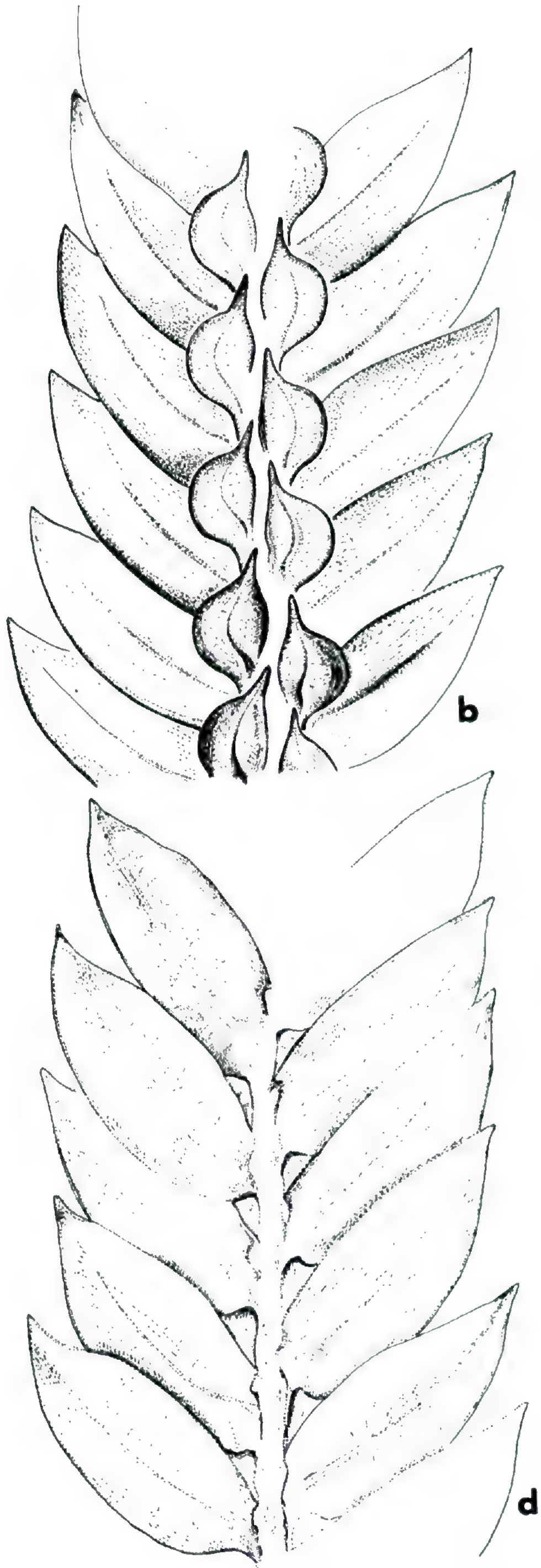


FIGURE 4—a. *Selaginella gigantea*. Lateral leaves from a portion of the ultimate branch-system, ventral view.—b. *S. exaltata* Lateral leaves from a portion of the ultimate branch-system, ventral view.—c. *S. gigantea*. lateral leaves from a portion of the ultimate branch-system, dorsal view.—d. *S. exaltata*. Lateral leaves from a portion of the ultimate branch-system, dorsal view.

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BOURRERIA RUBRA (BORAGINACEAE), A NEW SPECIES FROM COASTAL JALISCO, MEXICO

Bourreria rubra, a new species from coastal Jalisco, Mexico, is described and illustrated. The new species is distinguished by its shrubby habit, long slender pedicels, few-flowered inflorescences, short-petiolate oblanceolate leaves, and showy red flowers. It does not appear to be closely related to any other Mexican species.

Intensive collecting in the Estacion de Biologia Chamela (U.N.A.M.), Jalisco, and vicinity, and critical revision of these collections for a florula of the Station (Lott, in prep.) have resulted in the discovery of several novelties. Among these is a striking new red-flowered species of *Bourreria*.

Bourreria rubra E. J. Lott & J. S. Miller, sp. nov.

TYPE: Mexico. Jalisco: Mpio. La Huerta, Estacion de Biologia Chamela, ca. m 1,200 de la Vereda Tejon, en Selva Baja Caducifolia achaparrada, con dominante de *Plumeria rubra, Caesalpinia coriaria, Jatropha standleyi*. 22 Sept. 1981 (fl), *Lott 507* (holotype, MEXU; isotypes, CAS, GH, MO, US). Figure 1.

Frutex usque ad 3 m altus. Folia brevipetiolata, oblanceolata, strigillosa. Inflorescentia cymosa laxa, pedicellis ad 1.5–3.8 cm longis. Flores 1–7(–20); calyx campanulatus, sparse strigillosus, 5-lobatus, lobis acutis vel acuminatis, adaxialiter dense strigillosis; corolla rubra, late infundibuliformis, 1.4–2 cm longa; stamina exserta, filamentis in duabus tertiis partibus inferioribus hirsutis, alibi glabratis. Fructus globosus.

Shrub to 3 m, base 3 cm diam. or more, the bark gray, the stems pale, with scattered ovate lenticels ca. 0.5 mm long, strigose to glabrate. Leaves petiolate, alternate, the internodes mostly 1–2 cm long, or the leaves crowded on short shoots; blade oblanceolate, 2–6.5 cm long, 0.8–2.5 cm wide, the apex obtuse to acute, minutely apiculate with acumen 0.4–0.5 mm long, recurved abaxially, the base obtuse to slightly oblique, the sides more or less unequal, the margin entire, revolute, the upper surface scabrous and pustulate, more or less strigillose, shiny olive green, the lower surface sparsely strigillose and paler dull green, the midvein sulcate above, prominent beneath, the 4–7 pairs of secondary veins much less prominent; petiole 1–2 mm long, broadly sulcate on the adaxial surface, strigillose. Inflorescence terminal or subterminal, laxly cymose, sparsely strigose throughout; flowers 1–7 (–20), erect, bracts leaf-like, narrowly oblanceolate, 4–10 mm long, peduncle slender, mostly 0.3–1.5 cm long; pedicels slender, mostly 1.5–3.8 cm long, articulate at the base of the calyx, bracteoles linear to linear-lanceolate, 0.5–2 mm long, restricted to the lower one-fifth of the pedicel; calyx valvate, subglobose, acute in bud, 8–12 mm long at anthesis, short-stipitate, campanulate, with a few scattered strigillose hairs outside, the lobes 5, triangular, acute to acuminate, 3–4 mm long, 2–3 mm wide, subequal, thickened at the tips and densely white-strigillose within with hairs ca. 0.5 mm long; corolla red, broadly funnelform, 1.4–2 cm long, the tube 9 mm long, the lobes 5, rounded, 8–9 mm long, 4–7 mm wide, glandular-pubescent on the inner surface; stamens the same number as the corolla lobes, exserted, inserted on the corolla tube ca. 4 mm above the base, the filaments hirsute at and just above the point of insertion, with hairs ca. 0.6 mm long, the upper one-third glabrous, the free portion 6–9 mm long, the anthers oblong, 2–2.5 mm long, bithecous; ovary oblong, ca. 2 mm long, glabrous; disc annular; style ca. 11 mm long, bifid, the branches 3-5 mm long, stigmas capitate. Fruit bluish black, globose, ca. 8 mm diam., nutlets 4, ca. 6 mm long, ca. 4 mm wide, the outer surface rounded, deeply fluted with fine vertical ridges, the inner surface biconvex, dark reddish brown.

Additional specimens examined. MEXICO. JALISCO: Mpio. La Huerta, Estacion de Biologia Chamela, 11 Dec. 1983 (fr), *Lott 2177* (CHAPA, F, IBUG, MEXU); 12 Dec. 1983 (fl), *Miller 416* (MEXU, MO); 21 Feb. 1977 (fl) *Solis Magallanes 523* (MEXU); 20 Feb. 1981 (fl), *Solis Magallanes 2759* (F, MEXU); 2 Sept. 1981 (fl), *Solis Magallanes 3103* (GH, MEXU, MO, NY); 4 Nov. 1982 (fl), *Solis Magallanes 3928* (MEXU); Las Alamandas, centro turistico a 2.5 km al W de Quemaro, a 5 km al W de la carretera Puerto Vallarta-Barra de Navidad, 29 Oct. 1981 (fl, fr), *Lott 683* (CHAPA, MEXU, MO); 1 Aug. 1983 (fl, fr), *Lott et al. 1712* (CAS, ENCB, MEXU, MICH, MO, US).

Distribution. Thus far known only from the Estacion de Biologia Chamela and surrounding coastal area, the new species is apparently confined to tropical deciduous forest (Selva Baja Caducifolia) at 10–150 m elevation. Where exposed to constant strong coastal winds it forms part of a thick dwarf shrubby forest with *Bursera*

FIGURE 1. A, B. *Bourreria rubra* E. J. Lott & J. S. Miller.—A. Branch with inflorescence.—B. branchlet with fruits. Both from *Lott 683*.

instabilis, B. excelsa, Euphorbia schlechtendalii, Caesalpinia platyloba, and *Stenocereus* sp. Flowers are visited by Euglossine bees. Flowering and fruiting occur from August to February.

A genus in need of revision, *Bourreria* comprises nearly 50 species, all from the Neotropics (Airy Shaw, 1973). Perhaps 15 species occur in Mexico (Standley, 1924), but the genus is best represented in Cuba where there are probably close to 20 species. *Bourreria rubra* is unique in the genus in having red corollas. The majority of *Bourreria* species have either white- or cream-colored corollas although that of *B. quirosii* Standl. is pale yellow, and two species from Cuba, *B. moaensis* Britt. and *B. rostata* (DC.) Johnst., are reported to have bluish corollas (Leon & Alain, 1957). *Bourreria rubra* bears a superficial resemblance to the white-flowered *B. spathulata* (Miers) Hemsl. of Guerrero but differs in having longer and more slender pedicels, larger flowers, and essentially eglandular filaments. It is unusual among Mexican species in its densely shrubby habit, which resembles more closely that of many of the Cuban species, to which it is perhaps more closely allied than it is to any of the species known from Mexico or Central America.

We thank Fernando Chiang for the Latin diagnosis and F. Chiang and David Lorence for their comments on the manuscript. Elvia Esparza is gratefully acknowledged for her illustration, as is Arturo Solis Magallanes for the photographs that aided in preparation of the drawing.

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NOTES ON *DEINBOLLIA* SPECIES FROM CAMEROON

This note describes two new species of *Deinbollia* (Sapindaceae) from the Southwest Province of Cameroon and describes the fruit of *D. saligna* Keay for the first time. The collections were made by the author in the vicinity of the P.A.M.O.L. plantation, Ndian, which is the type locality for several river bank shrubs with very restricted ranges, including *D. saligna*. The two new species are closely related and differ from the rest of the genus in possessing only a single pair of large leaflets. One species is an unbranched shrub found in deep shade in the forest understorey, whereas the other is a bushy, stenophyllous shrub that grows on exposed, rocky river banks. A collection by De Wilde (# not known) from near Kribi, Centre-Sud Province, appears to be a third undescribed unijugate *Deinbollia* with distinctive, cordate leaflets.

Deinbollia unijuga D. W. Thomas, sp. nov. TYPE: Cameroon. Southwest Province: near Mundemba, 4°56′N, 8°55′E. Wet forest on steep river bank, ca. 1 km from Center Last Bush on path to Meka, ca. 50 m, 31 May 1984 (fl.), *Thomas 3496* (holotype, MO; isotypes, K, P, YA). Figure 1A–H.

Frutex ad 3 m altus, plerumque simplex, maturitate glaber. *Folia* alternata, petioli 1–4 cm longi, crassiculi, in sectione transversali triangulares, maturitate cinerei; foliola 2, opposita, glabra, coriacea, oblanceolata, 17–50 cm longa, 5–14 cm lata, apice acuminata, basi cuneata ad obtusa; petioluli crassi, ad 4 mm longi; costa prominens et carinata, nervis lateralibus principales 12–18. *Paniculae* inter folios ortae, plerumque laterales, densae puberulae, ad 6 cm longae, ramulis lateralibus paucis. *Flores* in cymis brevibus, bracteae parvae, triangulares, pedicellis 1 mm longis; sepala 5, late oblonga, 2–2.5 mm longa, extra puberula; petala 5, albida, obovata, 2.5 mm longa, 2 mm lata, marginibus pilosa, labium intus fimbriatum; stamina 8–12, per annulum circumcinctum, filamentis pilosis, 0.8 mm longis, antheris 0.8 mm longis; carpella 2–3. *Fructus* 1(–2) carpellorum compositus, flavus, circiter 1 cm diam.

A forest shrub to 3 m tall, though usually less than 1 m, usually unbranched. Leaves few, clustered at the branch tips, alternate, compound, glabrous when mature; petioles 1–4 cm long, stout and triangular in section, green when young, with smooth grey bark when mature; petiolule short (to 4 mm) and thick; leaflets 2, opposite, coriaceous, oblanceolate, 17–50 cm long, 5–14 cm wide, acuminate, base unequal, cuneate to obtuse, margin entire, slightly recurved, blades yellow-green above, paler below, midrib flat above, prominent and keeled below, main lateral nerves 12–18 pairs, looped close to the margin, reticulate venation prominent on both surfaces, blade yellow-green above, paler below. Inflorescences lateral, borne among the leaves. Panicles stout, to 6 cm long, with few short lateral branches, densely pubescent with short, stout, appressed, pale yellow hairs, cymes short, few-flowered. Bracts 0.5–1 mm, triangular, pedicels 1 mm. Sepals 5, imbricate, broadly oblong, 2–2.5 mm long, densely pubescent on the surfaces exposed in bud. Petals 5, white, obovate, 2.5 mm long, 2 mm wide, ciliate with a fringed lip within. Stamens 8–12, surrounded by an annulus, filaments pilose, 0.8 mm long, anthers 0.8 mm long. Ovary sparsely pubescent, of 2–3 carpels united at the base, style gynobasic, simple. Ripe fruit pale yellow, of 1 or 2 mericarps, each about 1 cm diam.; mesocarp pale, firm-textured, rather thin, endocarp not woody; embryos large and green, usually solitary.

Additional material examined. CAMEROON. SOUTHWEST PROVINCE: type locality, 10 July 1983 (fl. & imm. fr.), *Thomas 2208*; 5 km S of Ilor on Ekondo-Titi–Mundemba Road, forest on E side of road, 4°48′N, 8°54′E, 50 m, 20 Nov. 1983 (ripe fr.), *Thomas 2552*; 1 km S of Ekumbako, along forest footpath, 4°53′N, 8°53′E, 100 m, (sterile), *Thomas 2717*.

Deinbollia angustifolia D. W. Thomas, sp. nov. TYPE: Cameroon. Southwest Province: near Mundemba, 4°56′N, 8°52′E. Rocky bank of Idu River at Bulu on path to Ekumbako, 10 m, 7 Mar. 1984 (fl. & fr.), *Thomas 3253* (holotype, MO; isotypes, K, P, YA). Figure 1I–L.

Affinis *D. unijuga* D. W. Thomas. Frutex ad 1 m altus, ramus. Petioli 0.6–1.5 cm longi. Foliola 2, opposita, lineari-lanceolata, 10–30 cm longa, 0.8–2.2 cm lata, apex acuminata, basi cuneata. Paniculae sparse puberulae, ad 12 cm longae, plerumque terminales. Sepala vix puberula. Fructus circiter 1.5 cm diam.

This species is closely related to the preceding species and differs in the following characters: a much branched shrub of frequently inundated rocky river banks, to 1 m tall; petioles 0.6–1.5 cm long; leaflets linear-lanceolate, 10–30 cm long, 0.8–2.2 cm broad, base cuneate, panicles usually terminal, sparsely pubescent, to 12 cm long; se-

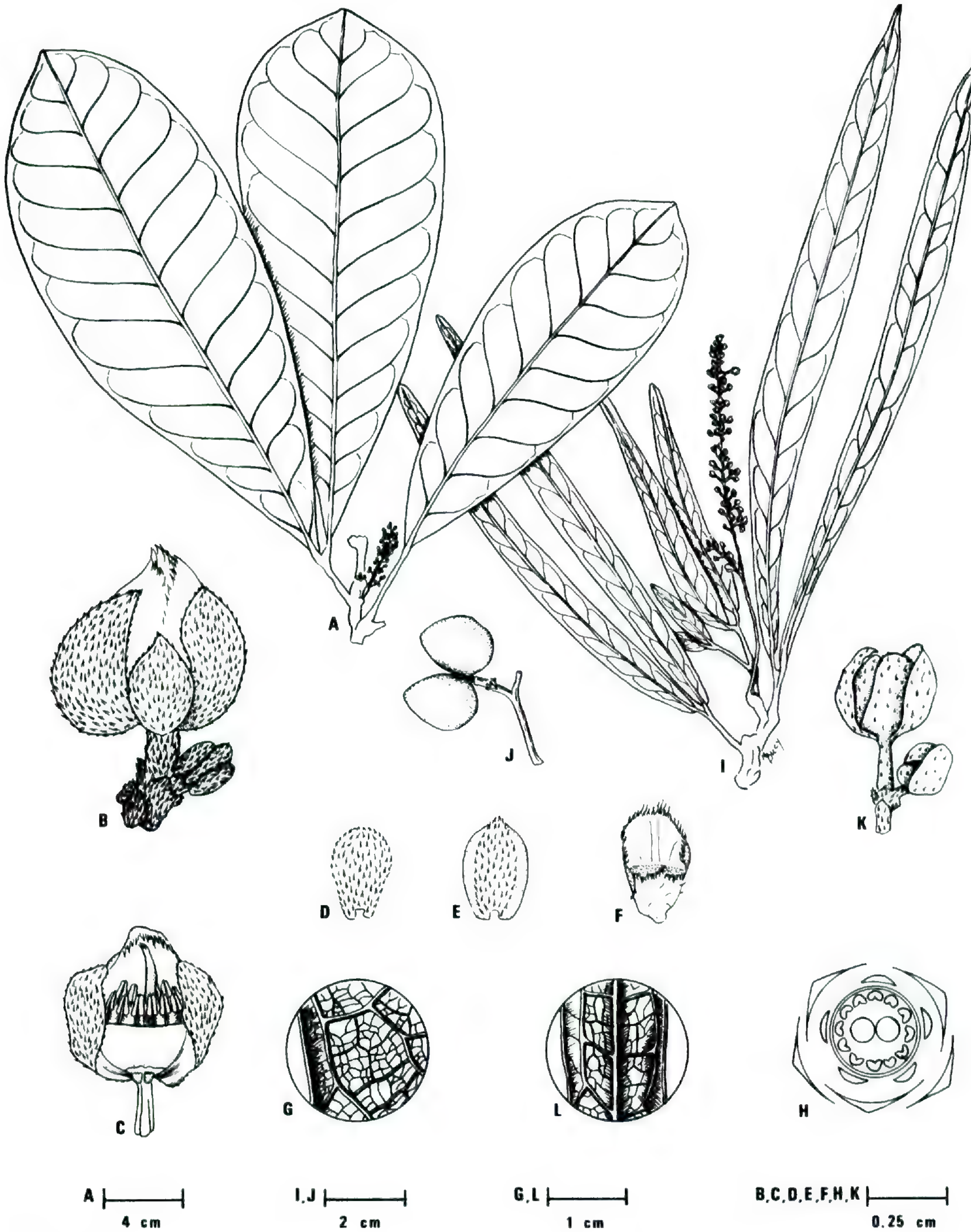

FIGURE 1. A–H. *Deinbollia unijuga* (*Thomas 2208*).—A. Branch, leaves, and inflorescence.—B. Flower.—C. Flower with two sepals and petals removed.—D, E. Sepals.—F. Petal interior.—G. Leaf margin.—H. floral diagram. I–L. *D. angustifolia*. (*Thomas 3497* except J)—I. Branch, leaves, and inflorescence.—J. Fruit (*Thomas 3253*).—K. Flower buds.—L. Leaf underside.

pals sparsely pubescent on the surfaces exposed in bud; ripe fruits ca. 1.5 cm diam.

Additional material examined. CAMEROON. SOUTHWEST PROVINCE: type locality, 1 June 1984 (fl.), *Thomas 3497*.

Deinbollia saligna Keay

Ripe fruits were collected from the type locality (banks of the Ndian River, less than 30 m elev.) by the author (*Thomas 2205*, 10 July 1983).

The mature fruit usually consists of a single mericarp with one or two aborted carpels at the base. Occasionally a second mericarp is present. The sepals are persistent but not enlarged. The mericarps are gibbous, glabrous, smooth, orange-colored and 1 cm in diameter. The mesocarp is yellow and firm-textured. Each mericarp contains one (rarely two) green embryos, which apparently begin germination on the parent plant.

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DATES OF PUBLICATION [VOLUMES 1 (1914)–72 (1985)]

CHERYL R. BAUER (COMPILER)

Listed below are the actual publication dates of the individual numbers in each volume of the *Annals of the Missouri Botanical Garden.* The publication date of each number was published in a subsequent number; those with question marks never have been printed in the journal itself, and at this time are not known. The entries followed with a date in brackets are ones where our records differ from the date we actually published as having been correct. In these cases, the date in brackets should be considered correct.

1	(1)	1–156.	1914.	???
	(2)	157–262.		1 July 1914
	(3)	263–356.		30 Sept. 1914
	(4)	357–432.		30 Jan. 1915
2	(1–2)	1–402.	1915.	17 May 1915
	(3)	403–658.		8 Oct. 1915
	(4)	659–841.		20 Dec. 1915
3	(1)	1–200.	1916.	7 July 1916
	(2)	201–308.		30 Sept. 1916
	(3)	309–402.		4 Nov. 1916
	(4)	403–517.		12 Jan. 1917
4	(1)	1–92.	1917.	9 Mar. 1917
	(2)	93–232.		???
	(3)	233–288.		20 Sept. 1917
	(4)	289–368.		8 Dec. 1917
5	(1)	1–108.	1918.	3 Apr. 1918
	(2)	109–176.		24 May 1918
	(3)	177–224.		20 Sept. 1918
	(4)	225–377.		23 Dec. 1918
6	(1)	1–92.	1919.	???
	(2)	93–170.		???
	(3)	171–252.		11 Oct. 1919
	(4)	253–320.		2 Mar. 1920
7	(1)	1–80.	1920.	???
	(2–3)	81–248.		8 Dec. 1920
	(4)	249–333.		???
8	(1)	1–96.	1921.	???
	(2)	97–236.		9 Jan. 1922
	(3)	237–342.		???
	(4)	343–400.		6 July 1922
9	(1)	1–78.	1922.	31 July 1922
	(2)	79–232.		27 Nov. 1922
	(3)	233–332.		16 Feb. 1923
	(4)	333–442.		???
10	(1)	1–110.	1923.	28 Sept. 1923
	(2)	111–190.		12 Oct. 1923
	(3)	191–298.		???
	(4)	299–427.		???
11	(1)	1–98.	1924.	25 July 1924
	(2–3)	99–388.		5 Jan. 1925
	(4)	389–465.		22 May 1925
12	(1)	1–132.	1925.	28 Sept. 1925
	(2)	133–212.		???
	(3)	213–358.		18 Feb. 1926
	(4)	359–424.		???
13	(1)	1–100.	1926.	8 May 1926
	(2)	101–172.		???
	(3)	173–354.		20 Sept. 1926
	(4)	355–489.		???
14	(1)	1–86.	1927.	8 June 1927
	(2)	87–210.		???
	(3)	211–358.		8 Oct. 1927
	(4)	359–436.		???
15	(1)	1–112.	1928.	30 Apr. 1928
	(2)	113–240.		???
	(3)	241–332.		???
	(4)	333–437.		22 Dec. 1928
16	(1)	1–128.	1929.	13 Mar. 1929
	(2)	129–226.		???
	(3)	227–388.		???
	(4)	389–519.		30 Dec. 1929
17	(1–2)	1–212.	1930.	14 May 1930
	(3–4)	213–476.		27 Dec. 1930
18	(1)	1–116.	1931.	???
	(2)	117–286.		30 June 1931
	(3)	287–488.		28 Oct. 1931
	(4)	489–612.		24 Dec. 1931
19	(1)	1–176.	1932.	15 Apr. 1932
	(2–3)	177–374.		23 July 1932
	(4)	375–538.		15 Nov. 1932
20	(1)	1–238.	1933.	29 Apr. 1933
	(2)	239–372.		10 July 1933
	(3)	373–568.		6 Oct. 1933
	(4)	569–817.		19 Dec. 1933
21	(1)	1–230.	1934.	12 Apr. 1934
	(2)	231–432.		5 June 1934
	(3)	433–608.		20 Sept. 1934
	(4)	609–719.		12 Dec. 1934
22	(1)	1–152.	1935.	25 Mar. 1935
	(2)	153–374.		25 May 1935
	(3)	375–758.		30 Sept. 1935
	(4)	759–874.		???
23	(1)	1–150.	1936.	20 Mar. 1936
	(2)	151–438.		10 June 1936
	(3)	439–526.		1 Sept. 1936
	(4)	527–662.		8 Jan. 1937
24	(1)	1–160.	1937.	20 Mar. 1937
	(2)	161–264.		30 Apr. 1937
	(3)	265–500.		27 Sept. 1937
	(4)	501–598.		23 Nov. 1937
25	(1)	1–454.	1938.	27 Dec. 1937
	(2)	455–728.		6 May 1938
	(3)	729–794.		28 Sept. 1938
	(4)	795–853.		28 Nov. 1938

ANN. MISSOURI BOT. GARD. 73: 222–224. 1986.

26	(1)	1–94.	1939.	???
	(2)	95–164.		29 Apr. 1939
	(3)	165–256.		???
	(4)	257–433.		30 Nov. 1939
27	(1)	1–118.	1940.	29 Feb. 1940
	(2)	119–258.		10 May 1940
	(3)	259–370.		25 Sept. 1940
	(4)	371–606.		10 Dec. 1940
28	(1)	1–146.	1941.	26 Feb. 1941
	(2)	147–248.		28 Apr. 1941
	(3)	249–374.		20 Sept. 1941
	(4)	375–532.		27 Nov. 1941
29	(1)	1–58.	1942.	18 Feb. 1942
	(2)	59–140.		20 Apr. 1942
	(3)	141–244.		18 Sept. 1942
	(4)	245–385.		18 Dec. 1942
30	(1)	1–96.	1943.	22 Mar. 1943
	(2)	97–280.		15 June 1943
	(3)	281–404.		30 Sept. 1943
	(4)	405–481.		20 Nov. 1943
31	(1)	1–172.	1944.	31 Mar. 1944
	(2)	173–234.		???
	(3)	235–300.		30 Sept. 1944
	(4)	301–419.		30 Nov. 1944
32	(1)	1–106.	1945.	28 Feb. 1945
	(2)	107–264.		???
	(3)	265–372.		15 Sept. 1945
	(4)	373–467.		30 Nov. 1945
33	(1)	1–140.	1946.	8 Mar. 1946
	(2)	141–248.		30 Apr. 1946
	(3)	249–314.		???
	(4)	315–408.		7 Dec. 1946
34	(1)	1–74.	1947.	29 Mar. 1947
	(2)	75–186.		???
	(3)	187–352.		31 Oct. 1947
	(4)	353–474.		???
35	(1)	1–106.	1948.	22 Mar. 1948
	(2)	107–192.		22 June 1948
	(3)	193–268.		20 Sept. 1948
	(4)	269–410.		???
36	(1)	1–132.	1949.	21 Mar. 1949
	(2)	133–258.		18 June 1949
	(3)	259–404.		30 Sept. 1949
	(4)	405–554.		30 Nov. 1949
37	(1)	1–120.	1950.	31 Mar. 1950
	(2)	121–314.		24 June 1950
	(3)	315–476.		30 Sept. 1950
	(4)	477–637.		15 Dec. 1950
38	(1)	1–94.	1951.	22 Mar. 1951
	(2)	95–206.		18 June 1951
	(3)	207–376.		5 Oct. 1951
	(4)	377–507.		31 Dec. 1951
39	(1)	1–96.	1952.	???
	(2)	97–172.		???
	(3)	173–254.		???
	(4)	255–353.		???
40	(1)	1–62.	1953.	???
	(2)	63–182.		???
	(3)	183–258.		30 Sept. 1953
	(4)	259–412.		18 Dec. 1953
41	(1)	1–212.	1954.	???
	(2)	213–262.		22 June 1954
	(3)	263–350.		???
	(4)	351–424.		???
42	(1)	1–102.	1955.	24 Mar. 1955
	(2)	103–194.		23 June 1955
	(3)	195–302.		17 Nov. 1955
	(4)	303–418.		???
43	(1)	1–86.	1956.	15 Apr. 1956
	(2)	87–252.		19 July 1956
	(3)	253–354.		31 Oct. 1956
	(4)	355–399.		22 Dec. 1956
44	(1)	1–124.	1957.	14 Mar. 1957
	(2)	125–194.		24 May 1957
	(3)	195–270.		9 Oct. 1957
	(4)	271–360.		29 Jan. 1958
45	(1)	1–92.	1958.	20 Mar. 1958
	(2)	93–202.		27 May 1958
	(3)	203–304.		28 Oct. 1958
	(4)	305–354.		6 Jan. 1959
46	(1–2)	1–194.	1959.	17 June 1959
	(3)	195–256.		15 Oct. 1959
	(4)	257–363.		28 Jan. 1960
47	(1)	1–80.	1960.	31 Mar. 1960
	(2)	81–204.		5 Aug. 1960
	(3)	205–262.		???
	(4)	263–372.		7 Feb. 1961
48	(1)	1–106.	1961.	3 Apr. 1961
	(2)	107–172.		???
	(3)	173–274.		28 Dec. 1961
	(4)	275–349.		19 Apr. 1962
49	(1–2)	1–136.	1962.	???
	(3–4)	137–259.		27 May 1963
50	(1–4)	1–54.	1963.	31 Jan. 1964
51	(1–4)	1–118.	1964.	30 Nov. 1964
52	(1)	1–98.	1965.	31 Mar. 1965
	(2)	99–222.		27 July 1965
	(3)	223–486.		15 Oct. 1965
	(4)	487–604.		5 Jan. 1966
53	(1)	1–114.	1966.	6 May 1966
	(2)	115–264.		7 Nov. 1966
	(3)	265–388.		30 Dec. 1966
54	(1)	1–94.	1967.	12 June 1967
	(2)	95–200.		27 Oct. 1967
	(3)	201–421.		11 Mar. 1968
55	(1)	1–80.	1968.	9 Sept. 1968
	(2)	81–170.		22 Oct. 1968
	(3)	171–402.		30 Apr. 1969
56	(1)	1–112.	1969.	13 Oct. 1969
	(2)	113–292.		18 Nov. 1969
	(3)	293–476.		17 July 1970
57	(1)	1–134.	1970.	2 Dec. 1970
	(2)	135–264.		16 Feb. 1971
	(3)	265–388.		14 June 1971

58	(1)	1–98.	1971.	14 July 1971
	(2)	99–266.		21 Jan. 1972
	(3)	267–369.		25 May 1972
59	(1)	1–104.	1972.	27 July 1972
	(2)	105–322.		28 Mar. 1973
	(3)	323–478.		15 May 1973
60	(1)	1–168.	1973.	22 Sept. 1973
	(2)	169–572.		19 Dec. 1973
	(3)	573–977.		3 July 1974
61	(1)	1–262.	1974.	8 Aug. 1974
	(2)	263–538.		11 Oct. 1974
	(3)	539–907.		24 Dec. 1974
62	(1)	1–224.	1975.	9 Apr. 1975
	(2)	225–514.		20 Aug. 1975
	(3)	515–834.		22 Jan. 1976 [19 Jan. 1976]
	(4)	835–1321.		17 Aug. 1976
63	(1)	1–208.	1976.	7 Sept. 1976
	(2)	209–384.		18 Jan. 1977
	(3)	385–656.		23 Mar. 1977
	(4)	657–895.		14 June 1977
64	(1)	1–144.	1977.	26 July 1977
	(2)	145–380.		2 Feb. 1978
	(3)	381–656.		26 May 1978
	(4)	657–748.		14 June 1978
65	(1)	1–366.	1978.	12 Oct. 1978
	(2)	367–782.		1 Feb. 1979
	(3)	783–998.		23 Mar. 1979
	(4)	999–1258.		13 Aug. 1979
66	(1)	1–108.	1979.	13 Aug. 1979 [29 Aug. 1979]
	(2)	109–276.		10 Oct. 1979
	(3)	277–590.		15 Jan. 1980
	(4)	591–903.		22 Feb. 1980
67	(1)	1–256.	1980.	12 Mar. 1980
	(2)	257–522.		2 May 1980
	(3)	523–818.		??? [4 Mar. 1981]
	(4)	819–1059.		29 June 1981
68	(1)	1–232.	1981.	17 Nov. 1981
	(2)	233–378.		20 Jan. 1982
	(3)	379–504.		4 Mar. 1982
	(4)	505–686.		29 Mar. 1982
69	(1)	1–238.	1982.	15 Dec. 1982 [16 Dec. 1982]
	(2)	239–430.		5 Jan. 1983
	(3)	431–734.		3 June 1983
	(4)	735–998.		8 Aug. 1983
70	(1)	1–210.	1983.	14 Nov. 1983
	(2)	211–420.		4 Apr. 1984
	(3)	421–576.		17 July 1984
	(4)	577–749.		9 Oct. 1984
71	(1)	1–346.	1984.	31 Dec. 1984
	(2)	347–630.		19 Mar. 1985
	(3)	631–986.		19 Apr. 1985
	(4)	987–1187.		14 May 1985
72	(1)	1–166.	1985.	10 June 1985
	(2)	167–450.		19 July 1985
	(3)	451–590.		30 Aug. 1985
	(4)	591–880.		5 Nov. 1985

ERRATA

The acronym MAD is used erroneously for TAN in the paper titled "A Monograph of the Monimiaceae (Laurales) in the Malagasy Region (Southwest Indian Ocean)," by David H. Lorence [72(1): 1–165. 1985].

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Contents continued from front cover

Catalog of the Mosses of China *Paul L. Redfearn & P.-C. Wu* ... 177

NOTES

A Remarkable New *Selaginella* from Venezuela *Julian A. Steyermark & Alan R. Smith* ... 208

Bourreria rubra (Boraginaceae), a New Species from Coastal Jalisco, Mexico *Emily J. Lott & James S. Miller* ... 216

Notes on *Deinbollia* Species from Cameroon *Duncan W. Thomas* ... 219

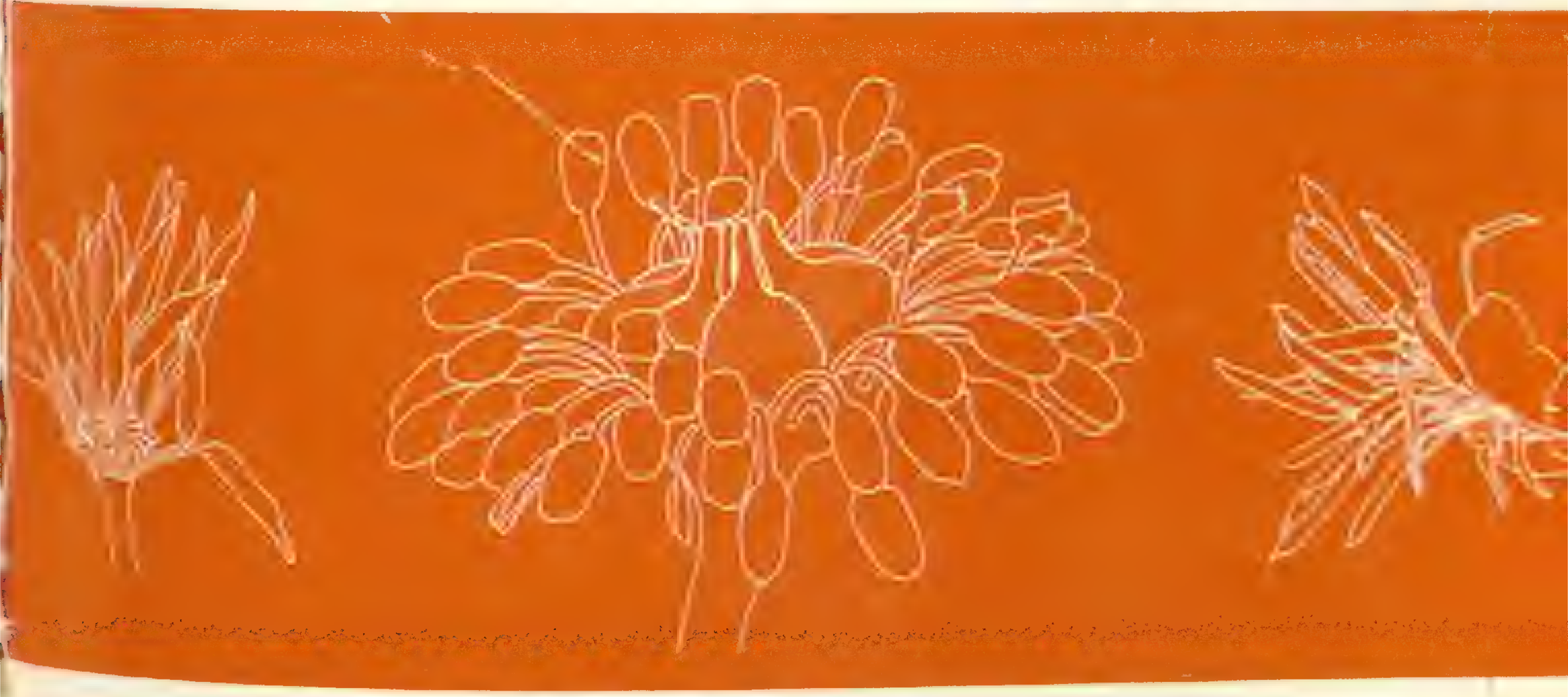
Dates of Publication *Cheryl R. Bauer* ... 222

ERRATA ... 224

Cover picture. Until 1982 the public entrance to the Garden was located on Tower Grove Ave... at Flora Place. The original structure, designed by English-born St. Louis architect George I. Barn... featured four massive rusticated columns on the exterior and corinthian columns on the interior. T... exterior entablature carried the name "Missouri Botanical Garden 1858." The gate was extensiv... reworked and greatly enlarged in 1920 by James P. Jamieson. Modified dome columns and pilast... replaced the originals. Barnett's original engraved name was reformatted into three lines and re... in a pediment immediately above the center of the structure. The Main Gate was replaced in 19... by the Ridgway Center, located on Shaw Boulevard, and renamed Flora Gate. The rooms to the ... of the gate proper are used for public meetings, and the area to the right contains storage and ... rooms.

ANNALS OF THE MISSOURI BOTANICAL GARDEN

VOLUME 73 1986 NUMBER 2



CONTENTS

Phylogeny of the Hamamelidae: An Introduction *David L. Dilcher & Michael S. Zavada* 225

Commentary on the Status of the Hamamelidae *Arthur Cronquist* 227

Evolution of the Fagaceae: The Implications of Foliar Features *Jay H. Jones* 228

Fossil Evidence Regarding the Evolution of *Nothofagus* Blume *Edgardo J. Romero* 276

Evolution and Reproductive Biology of Inflorescences in *Lithocarpus*, *Castanopsis*, *Castanea*, and *Quercus* (Fagaceae) *Robert B. Kaul* 284

Floral Structure, Systematics, and Phylogeny in Trochodendrales *Peter K. Endress* 297

The Floral Morphology and Vascular Anatomy of the Hamamelidaceae: Subfamily Liquidambaroideae *A. Linn Bogle* 325

Comparative Pollen Morphology and Its Relationship to Phylogeny of Pollen in the Hamamelidae *Michael S. Zavada & David L. Dilcher* 348

Morphology and Development of Pistillate Inflorescences in Extant and Fossil Cercidiphyllaceae *Peter R. Crane & Ruth A. Stockey* ... 382

Fruit and Seed Dispersal and the Evolution of the Hamamelidae *Bruce H. Tiffney* 394

Contents continued on back cover

VOLUME 73
SUMMER 1986
NUMBER 2

ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

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VOLUME 73 1986 NUMBER 2

PHYLOGENY OF THE HAMAMELIDAE: AN INTRODUCTION

The collection of papers published in this issue of the Annals of the Missouri Botanical Garden are primarily those papers delivered at a symposium, Phylogeny of the Hamamelidae, presented at the annual meeting of the Botanical Society of America, August 5–9, 1984, in Fort Collins, Colorado.

The Superorder Amentiferae presented by Takhtajan in 1959 and later recognized as the subclass Hamamelididae by him in 1969 was adopted by Cronquist (1981) in his presentation of the subclass Hamamelidae. The roots of this classification lie in the early recognition by nineteenth century systematic botanists that these plants share many similar features and may be considered a natural group (Engler, 1886; Stern, 1973). Stern (1973) presented detailed documentation of the history of the "Amentiferous Concept." The papers published in this symposium volume present an overview of several aspects of this group of plants.

With a few exceptions (Thorne, 1973, 1983), most researchers recognize the Hamamelidae as a grouping of closely-related plants. The questions that exist concerning the phylogeny of the Hamamelidae are: Can this group of plants still be considered a natural group if examined in detail by new methods and techniques? What can detailed analysis of particular orders or families tell us about the relationships within these taxa and between them and related orders or families? Can we develop a clear understanding of primitive versus advanced character states in the Hamamelidae? The papers presented in this symposium volume address many of these questions.

It is clear that some taxa of the Hamamelidae are very ancient. The subclass can be recognized back into the Lower Cretaceous (Upchurch, 1984; Dilcher & Eriksen, 1983). Also other taxa, such as the Chloranthaceae, that were once considered to be very closely related to this group (Engler, 1886), have been reported from the Lower Cretaceous based upon pollen data and leaf data (Walker & Walker, 1984; Upchurch, 1984). The very early occurrence of taxa that bear so-called reduced simple flowers (Dilcher, 1979; Dilcher & Eriksen, 1983), as illustrated by platanoid fossil flowers and fruits from the Lower Cretaceous, raises a basic question about the extent of floral elaborations versus floral reductions as important factors in floral evolution. It is clear that at least some very early angiosperms had very small flowers. This may have been much more common than was previously thought. Certainly, floral elaborations as well as reductions of floral parts played a significant role in evolution of the various taxa of the Hamamelidae.

Many of the taxa in this subclass are effectively wind pollinated, some accommodate both anemophily and entomophily, and a few taxa are exclusively entomophilous (Faegri & van der Pijl, 1978). Pollination by wind has changed very little, if at all, since the Cretaceous and probably the insect vectors of the pollen in the Hamamelidae have changed very little as well. Therefore, in the absence of pressures to change their reproductive structures, the Hamamelidae probably represent one group of flowering plants that has changed very little since the end of the Cretaceous with the exceptions of extinctions of taxa and radiations resulting from animal dispersal

Ann. Missouri Bot. Gard. 73: 225–226. 1986.

of fruits and seeds (Tiffney, 1984). This is why the Hamamelidae are such an excellent group to use in testing hypotheses of angiosperm evolution. In addition, because of the abundant fossil representation of the group and the availability of many of the extant taxa in the populated areas of the Northern and Southern Hemispheres, it should continue to yield useful data on angiosperm evolution and phylogeny.

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COMMENTARY ON THE STATUS OF THE HAMAMELIDAE

ARTHUR CRONQUIST[1]

Some years ago there was a symposium at the AIBS meetings in Amherst, called "What ever happened to the Amentiferae?" My joking answer at the time was, "They are alive and well under the name Hamamelidae." A few of Engler's families, notably the Salicaceae, have been pruned off, but the bulk of the group remains together as Engler had it. Most of us now believe that the group has reduced rather than primitively simple flowers, and therefore a basal position within the dicots is no longer supported. Still, Engler would feel quite at home with the Hamamelidae as now conceived.

The frequent reference in papers of the present symposium to the "Hamamelidae of Cronquist" makes me a bit uneasy. I stand by the interpretation I presented in 1981, only slightly modified from that of 1968, but I cannot take too much credit for it. The phyletic diagram at the back of Takhtajan's German-language book of 1959 clearly shows the Hamamelidae (minus the Salicales) as a unified though nameless clade derived from the Magnoliales. He formally established and named the Hamamelidae in his Russian-language book of 1966. I well remember his pointing out to me (in 1965) the phyletic significance of the distally unsealed carpel in *Platanus*.

The papers in the present symposium reflect a perfectly normal evolution of taxonomic thought regarding the Hamamelidae. I can take some comfort in the degree to which the data and their interpretation are compatible with my 1981 scheme. It is interesting that Zavada and Dilcher (1986) consider that the pollen morphology supports inclusion of the Daphniphyllales, Juglandales, Leitneriales, and Urticales in the Hamamelidae. The position of all of these has been questioned (and sometimes vigorously debated) by other authors. *Leitneria*, in particular, has recently been associated on serological grounds with families of the Sapindales (Petersen & Fairbrothers, 1983).

I take note of Giannasi's (1986) reference to the effort by Kubitzki and Gottlieb (1984) to present a general scheme for the evolution of secondary metabolites in the angiosperms. He is quite right that if that scheme is accepted, then the status of the Hamamelidae as derived from the Magnoliidae must be questioned. I intend to present a different scheme for secondary metabolites in a forthcoming book.

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EVOLUTION OF THE FAGACEAE: THE IMPLICATIONS OF FOLIAR FEATURES[1]

JAY H. JONES[2]

ABSTRACT

The leaf architecture and cuticular morphology of extant Fagaceae have been examined and compared to those of putatively fagaceous fossil forms. The various leaf types found among extant Fagaceae appear at different times in the fossil record. The most recent types to evolve are typical lobed oak forms (Oligocene-Miocene) whereas coarsely toothed oaks and regularly craspedodromous chestnut-like leaves are found as early as the Eocene. There are no leaf forms directly comparable to modern Fagaceae in pre-Eocene sediments but the presence of well defined vegetative and reproductive materials of two distinct modern subfamilies in the Eocene suggests that this family arose in or before the Paleocene. Leaf forms generally comparable to those of the Fagaceae do occur in the Paleocene. The characteristics of these early forms, especially those of the secondary venation and margin, suggest a common origin with the Betulaceae and reaffirm the close affinity of these two families. *Nothofagus* leaves are distinct from those of all other Fagaceae suggesting that this taxon should be considered a separate family as proposed by Kuprianova and Nixon on other grounds. Nothofagaceae also seem to be closely related to the Betulaceae and probably arose from the same fagalean stock. Suggestions that modern lobed oaks are atavistic expressions of primitive palmately lobed-compound forms, variously assigned to *Debeya, Dewalquea,* and *Araliopsis,* although possibly correct, are poorly supported by foliar data. Foliar features also fail to provide convincing support for the origin of the Fagaceae from Cretaceous platanoids.

The Fagaceae comprise a large and important family of trees and shrubs (Lawrence, 1951), yet we know little about their evolution. The fossil record of the family reportedly extends back to the Cretaceous (Berry, 1923) but pre-Tertiary records have been questioned in recent years (Wolfe, 1973). Nineteenth and early twentieth century reports are especially questionable because they usually were based on the superficial resemblance of fossil materials, most commonly leaves, with those of extant plants (Dilcher, 1973, 1974). Because any complete evolutionary study must include information from both fossil and modern organisms (Simpson, 1953; Wolfe, 1973), it is important to study fossil materials in sufficient detail to assure accurate taxonomic placement. This requires not only a detailed study of the fossil material but also a detailed knowledge of the nature and variation of the same characters in similar modern plants. Much work has been done on modern Fagaceae (Trelease, 1924; Camus, 1928–1929, 1934–1954; Brett, 1964; Forman, 1966a; Elias, 1971; Soepadmo, 1972; and others), yet even Camus, in her monumental monographs of the chestnuts and oaks (1928–1929; 1934–1954), did not provide much of the information on foliar characteristics necessary for the proper interpretation of fossil leaves. A primary objective of the research upon which this paper is based (Jones, 1984) was to examine thoroughly the foliar characteristics of extant Fagaceae using modern methods of leaf architectural and cuticular analyses (Stace, 1965; Hickey, 1973, 1977, 1979; Dilcher, 1974; Hickey & Wolfe, 1975). Information obtained from this study (Jones, 1984) has provided a basis for the interpretation of putatively fagaceous fossil leaves as well as useful information for testing classification schemes of modern Fagaceae, which are based primarily on nonfoliar features.

The goal of this paper is to integrate newly acquired foliar information with other vegetative, reproductive, and fossil information in order to provide a view of the evolution of and

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within the Fagaceae. Past taxonomic treatments of the Fagaceae are reviewed first, followed by a discussion of the classification and evolutionary history of each genus with emphasis on the contribution of foliar information. Discussion of reproductive aspects, although taken into consideration, has been kept to a minimum because these have been reviewed in great detail elsewhere (Hjelmqvist, 1948; Brett, 1964; Forman, 1964a, 1966a, 1966b; Soepadmo, 1968a, 1968b, 1970; Abbe, 1974; Fey & Endress, 1983; Kaul & Abbe, 1984). The final section of this paper provides an assessment of the contribution of foliar information to classification, primarily above the generic level, and to understanding of the origin and evolution of the family within the Amentiferae. Keys for confirming fagaceous affinities among hamamelidopsid leaf materials and generic affinities within the Fagaceae are found in Appendix I and Appendix II respectively. Illustrations and descriptions of trichome types found in this family are presented in Appendix III.

Taxonomic Review of the Fagaceae

The constituent genera of the Fagaceae have been surveyed in numerous works. From the time of Ray (1682, 1703) members of the genera *Quercus, Fagus,* and *Castanea* have been grouped with other amentiferous plants (Stern, 1973). De Jussieu (1789) formalized the concept of the Amentiferae and included the above genera in the "order" Amentaceae. Dumortier in 1829 was allegedly the first to recognize the family (Soepadmo, 1972), and de Candolle (1868) was the first to circumscribe the family in its present form. He applied the name Cupuliferae, which has been used since in numerous ways by various authors. Oersted (1871) subdivided the Cupuliferae, used here at the familial level, into three subfamilies along lines approximating those drawn by recent students of this family (e.g., Forman, 1966a). Bentham and Hooker (1880) treated the Cupuliferae as an "order" with three tribes. The circumscription of the tribe Quercineae conforms to that of the Fagaceae of modern authors. However, Bentham and Hooker did not subdivide this tribe further, above the generic level, and thus their scheme does not provide taxa corresponding to modern subfamilies. The name Fagaceae was first used by Prantl (1894), who absorbed the "subfamily" Quercineae, sensu Oersted, into the Castaneae and reduced the number of genera in the family from seven to five. Brett (1964) retained Prantl's subfamilial classification but recognized, at least tacitly, nine genera. Schwarz (1936a) appears to be the most extreme "splitter" among western botanists. He recognized 11 genera distributed among the traditional three subfamilies. With the possible exception of Schwarz, modern treatments of the Fagaceae are remarkably uniform in spite of significant intrageneric variability and the remarkable similarity between some elements of different genera. The suprageneric classifications of Forman (1966a), Hutchinson (1967), and Elias (1971) are identical. Melchior's (1964) system differs in that the genus *Trigonobalanus* is placed in the Fagoideae rather than the Quercoideae. Lozano-C. et al. (1979), in a report of a third species of *Trigonobalanus,* established a fourth subfamily, the Trigonobalanoideae, to accommodate this problematic genus. Most recently Smiley and Huggins (1981) adopted Forman's (1966a) classification with the addition of the subfamily Pseudofagineae to house the fossil genus *Pseudofagus.* The analysis of another fossil form (Manchester & Crane, 1983), *Fagopsis,* presented an equally good case for the erection of a new subfamily if not a new family. However, none was proposed by the authors. The recognition of *Nothofagus* as a separate family, first proposed by Kuprianova (1962), also seems to be gaining support (Nixon, 1982), but no comprehensive scheme of classification containing this innovation has been published. A summary of the more important classification schemes, together with a proposed classification based on the integration of foliar information, is found in Table 1.

Generic Analyses

FAGUS L.

The genus *Fagus* exhibits very little morphological variation. This is not only true of leaves (Jones, 1984) but also extends to reproductive features (see, for example, Praglowski, 1982) and nonfoliar vegetative features such as wood (Shimaji, 1962). The homogeneity of this genus has apparently made it an unattractive candidate for monography. It is the only genus of Fagaceae for which there is no recent comprehensive monograph. The most complete recent works dealing with *Fagus* are the palynological studies of Hanks and Fairbrothers (1976) and Praglowski (1982). No formal subgeneric groups of *Fagus* species have been established in these or other works.

TABLE 1. Taxonomic treatment of fagaceous plants by various authors. Inclusions noted are relative to the classification of Forman (1966a) and others.

de Candolle 1868

Family Cupuliferae
Fagus (incl. some *Nothofagus*)
Nothofagus
Castanea
Castanopsis (incl. *Chrysolepis*)
Quercus (incl. *Lithocarpus*)

Oersted 1871

Family Cupuliferae
Subfamily Fagineae
Fagus
Nothofagus
Subfamily Castaninae
Castanea (incl. *Castanopsis* & *Chrysolepis*)
Pasania
Cyclobalanus (incl. *Lithocarpus*)
Subfamily Quercineae
Quercus
Cyclobalanopsis

Prantl 1894

Family Fagaceae
"Subfamily" Fageae
Fagus
Nothofagus
"Subfamily" Castaneae
Castanea (incl. *Castanopsis* & *Chrysolepis*)
Pasania
Quercus

Schwarz 1936a

Family "Cupuliferae"
Subfamily Fagoideae
Fagus
Nothofagus
Subfamily Castaneoideae
Tribe Castaneae
Castanea
Castanopsis (incl. *Chrysolepis*)
Tribe Pasanieae
Pasania
Cyclobalanus
Lithocarpus
Subfamily Quercoideae
Tribe Cyclobalanopsideae
Cyclobalanopsis
Erythrobalanus
Tribe Querceae
Macrobalanus
Quercus

TABLE 1. Continued.

Brett 1964

Family Fagaceae
Subfamily Fagoideae
Fagus
Nothofagus
Subfamily Castaneoideae
Tribe Castaneae
Castanea
Chrysolepis
Castanopsis
Tribe Lithocarpeae
Lithocarpus
Tribe Pasanieae
Pasania
Tribe Querceae
Quercus
Cyclobalanopsis

Melchior 1964

Family Fagaceae
Subfamily Fagoideae
Fagus
Nothofagus
Trigonobalanus
Subfamily Castaneoideae
Tribe Castaneae
Castanea
Castanopsis (incl. *Chrysolepis*)
Tribe Pasanieae
Pasania
Lithocarpus
Subfamily Quercoideae
Quercus

Hutchinson 1967
Elias 1971

Family Fagaceae
Subfamily Fagoideae
Fagus
Nothofagus
Subfamily Castaneoideae
Castanea
Castanopsis
Chrysolepis
Lithocarpus (*Pasania*)
Subfamily Quercoideae
Quercus
Trigonobalanus

Soepadmo 1972
Forman 1966a

Family Fagaceae
Subfamily Fagoideae
Fagus
Nothofagus

TABLE 1. Continued.

Subfamily Castaneoideae
Castanea
Castanopsis (incl. *Chrysolepis*)
Lithocarpus
Subfamily Quercoideae
Quercus
Trigonobalanus

Lozano-C. et al. 1979
Family Fagaceae
Subfamily Fagoideae
Fagus
Nothofagus
Subfamily Castaneoideae
Castanea
Castanopsis
Lithocarpus
Chrysolepis
Subfamily Quercoideae
Quercus
Subfamily Trigonobalanoideae
Trigonobalanus

Smiley and Huggins 1981
Family Fagaceae
Subfamily Fagoideae
Fagus
Nothofagus
Subfamily Pseudofagineae
Pseudofagus
Subfamily Castaneoideae
Castanea
Castanopsis
Lithocarpus
Subfamily Quercoideae
Quercus
Trigonobalanus

Present Study
Family Nothofagaceae
Nothofagus
Family Fagaceae
Subfamily Fagoideae
Fagus
Subfamily Castaneoideae
Castanea
Chrysolepis
Castanopsis
Lithocarpus
Subfamily Trigonobalanoideae
Trigonobalanus
Subfamily Quercoideae
Quercus

Paleobotanists have made informal groupings based on relatively minor differences in leaf characteristics. Tralau (1962), for example, divided the beeches into *Fagus* 'grandifolia' and 'sylvatica' types in his investigation of fossil *Fagus* from Europe. Pollen data seem to at least partially support this distinction (see Praglowski, 1982). Tanai (1974) distinguished three groups based primarily on a leaf index (i.e., length/width × 100) and the number of secondary veins but again avoided the establishment of any formal infrageneric taxa. Tralau (1962) suggested that the 'sylvatica' and 'longipetiolata' groups intergrade and are best considered as one. If it were not for geographical separation this intergradation might apply to the 'sylvatica' and 'grandifolia' groups as well. In fact, Hanks and Fairbrothers (1976) found that none of the groups proposed by Tralau (1962) and Tanai (1974) clustered tightly on the basis of pollen features. The lack of formal subgeneric taxa, therefore, seems quite reasonable.

Foliar information confirms the relative uniformity within this genus and can be used only in a very limited fashion for classification below the generic level (as in Cooper & Mercer, 1977). The observed intraspecific variation in foliar characteristics often exceeds interspecific variation. There are no clear cut qualitative differences that can be used to distinguish subgroups. In contrast, foliar information is very useful for the recognition of *Fagus,* whose leaves can be distinguished from those of other amentiferous families as well as other genera of Fagaceae (Appendices I and II). The margin, secondary venation, intercellular ridge sinuosity of the upper cuticle, and rather restricted complement of trichome types (see Text-Fig. 1 and Appendix III) are the most characteristic features of these leaves (Jones, 1984).

The fossil record of *Fagus* was thought to extend far back into the Cretaceous (Berry, 1923). However, most reports of Cretaceous *Fagus* have been based on isolated leaves that are often poorly preserved and frequently bear only a superficial resemblance to those of *Fagus* (see Lesquereux, 1874). Some describe leaves that do not even resemble modern *Fagus.* Others describe leaves from sediments that have been shown to be much younger than originally thought. Wolfe (1973) suggested that there are no valid reports of any Fagaceae prior to the Paleocene. Muller (1981) suggested that the earliest reliable pollen record is that of *Fagus granulata* (Piel, 1971) from the Lower Oligocene of Canada. There are

	Fagus	*Nothofagus*				*Castanea*	*Chrysolepis*	*Castanopsis*	*Lithocarpus*	*Trigonobalanus*	*Quercus*						
		I	*II*	*III*	*IV*						Cyclobalanopsis	Cerris	Mesobalanus	Lepidobalanus	Macrobalanus	Protobalanus	Erythrobalanus
Unicellular																	
1. Solitary	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
2. Conical	●	●	●	●	●	●		●	●	●							
3. Papillae									●		●						
4. Appressed laterally attached											●						●
5. Fasciculate						●		●	●	●	●[1]	●	●	●	●	●	●
6. Stellate						●	●		●		●[1]	●	●	●		●	●
7. Fused Stellate									●		●[1]	●		●			
8. Stipitate fasciculate									●		●[1]	●	●	●			●
9. Appressed parellel tuft									●								
10. Multiradiate									●								●
Intermediate																	
11. "Thick"-walled peltate							●										
12. Curly thin-walled					●												
13. "Thin"-walled peltate								●	●								
14. Rosulate									●		●[1]	●					●
Glandular																	
15. Simple uniseriate	●					●			●	●	●	●	●	●	●	●	●
16. Capitate or irregularly multiseriate						●						●	●	●	●	●	●
17. Large globular		●	●	●													
18. Branched uniseriate								●[2]	●	●		●[1]	●		●	●	
19. "Glandular" peltate										●							

TEXT-FIGURE 1. Distribution of trichome types within the Fagaceae. See Appendix III for thorough descriptions and illustrations of each type. [1]Not observed in this study but reported in Camus (1934–1954). [2]Not observed in this study but reported in Camus (1928–1929).

reports of earlier occurrences that may be accurate but need to be studied further. For example, Krutzsch (1970) reported fagoid pollen from the Eocene of Europe, but provided neither detailed descriptions nor figures. Kedves (1967) also reported fagoid pollen from the Eocene of Europe. Pollen with the general form of that from *Fagus* has been reported from late Cretaceous sediments (Srivastava, 1969; Jarzen & Norris, 1975) but Muller (1981) has rejected these as not representing *Fagus*. *Fagus*-like wood has been reported from the Upper Cretaceous of Japan

(Stopes & Fuji, 1910), the Lower Senonian of western Germany (Vater, 1884), and other European and North American localities. There is also one unconfirmed report of *Fagus* wood from South America (Salard, 1961). The first presumed fruits of *Fagus* appear to be those reported from the Middle–Upper Eocene "Wilcox" Flora of southeastern North America (Lesquereux, 1859). This report is based solely on gross external features and no subsequent reports of *Fagus* fruits have been made in spite of continuing work in the area. Brown (1944) considered a quadripartite structure, previously assigned to *Diospyros aspera* Berry, to be a *Fagus* cupule but Berry (1945) vigorously refuted the reassignment of this form. Brown (1944) also associated the fossil leaf form *Dryophyllum tennesseense* with the purported *Fagus* cupules. Upon reexamination, however, these leaves have been shown clearly not to be *Fagus* but rather a castaneoid type most likely associated with the genus *Castanea* (Jones, 1984). Thus, this report of Eocene *Fagus* is questionable. Manchester and Crane (1983) suggested that there are no confirmed reports of *Fagus* earlier than the Oligocene, yet, Takhtajan (1982) presented Eocene and even some Upper Paleocene records. There are certainly valid reports of this genus in the Oligocene (e.g., Conwentz, 1886; Chandler, 1957), and there are numerous reports of beech leaves and fruits in the Neogene (Unger, 1850; Kirchheimer, 1957; Tralau, 1962; Tanai, 1974; Van der Burgh, 1978a; Smiley & Huggins, 1981; Takhtajan, 1982). In summary, the fossil evidence currently available suggests that *Fagus* had evolved, certainly by the Oligocene, and perhaps as early as the Upper Paleocene.

The geographical distribution of *Fagus* ranges discontinuously over most temperate areas of the Northern Hemisphere. It is notably absent in some areas, such as western North America, where it is found only in the fossil record. There are no native *Fagus* in the Southern Hemisphere and reports of fossil *Fagus* from there are most likely in error. Many early reports result from the historical assignment of *Nothofagus* forms to the genus *Fagus* (see Ettingshausen, 1891). Others probably result from misidentifications based on superficial resemblances between *Fagus* and architecturally similar leaf forms such as *N. alessandrii.* In the Northern Hemisphere, *Fagus* appears to have been uniformly distributed over the major land masses with Neogene occurrences even in Alaska (Hollick, 1936) and Greenland (Heer, 1883). The distribution of forms has undergone considerable contraction, particularly during the Pleistocene.

The origin of *Fagus* appears to have been in the Northern Hemisphere (Berry, 1923). Hanks and Fairbrothers (1976) placed the site of origin in south central Asia but Tanai (1974) reported older *Fagus* fossils from North America, implying a North American origin. Takhtajan's (1982) reports of Oligocene, Eocene, and Upper Paleocene *Fagus* in Asia, together with greater diversity, tend to support an Asian origin. In his 1969 treatise on the origin of flowering plants, Takhtajan in fact, explicitly suggested an east Asian origin for *Fagus.* Van Steenis (1971a) is more specific, asserting that the Fagoideae arose somewhere between Yunnan and Queensland with *Fagus* radiating from the Northern part of the region. Opponents (e.g., Schuster, 1972), have contended that the region circumscribed by van Steenis is not consistent with current geological interpretations, which suggest that this area was widely separated until the late Tertiary. Although van Steenis' hypothesis has largely been dismissed, the site of origin for *Fagus* is still a subject of debate.

A recent paper by Hickey et al. (1983) is particularly germane to the discussion of centers of origin. These authors suggested that, on the basis of new paleomagnetic data, the age assessments of many high latitude floras, modified in recent years on the basis of paleofloristic similarities with "younger" floras of lower latitudes, may be as old as originally thought. If their conclusions are accurate, many plants and terrestrial animals occur at high latitudes up to 18 million years before they occur at mid-latitudes. Although there has been much concern over some of the paleomagnetic and other interpretations made in this particular study (Kent et al., 1984; Norris & Miall, 1984; Hickey et al., 1984), the once popular belief that temperate floral elements differentiated at high latitudes may be valid for many species. It seems that *Fagus* fits this pattern very well. I find this hypothesis to be very appealing but a better knowledge of the fossil floras of southeast Asia as well as those of higher latitudes is needed to confirm or refute it.

Both Tralau (1962) and Tanai (1974) found *Fagus grandifolia*-like fossils antedating the *F. sylvatica* types. The *F. grandifolia*-like forms are also the most widely distributed, occurring in the fossil record of Europe, Asia, and North America until the end of the Tertiary. The *F. sylvatica* and

F. longipetiolata types have not been found outside Europe and Asia. At the end of the Tertiary the 'grandifolia' types became extinct in all but North America. Available paleobotanical data therefore, indicate that the 'grandifolia' type is primitive within the genus *Fagus*.

Foliar data, from extant plants, do not contribute much to the identification of a primitive form within the genus. The basic leaf architecture (i.e., characteristics of the margin, secondary veins, and gross form) of *F. grandifolia* approaches those of some species in the Castaneoideae and Quercoideae more closely than the 'sylvatica' or 'longipetiolata' types do, but such similarity in form is probably best explained by convergence rather than close proximity to a common ancestral form.

NOTHOFAGUS BLUME

Unlike *Fagus, Nothofagus* is not tightly bound together as a group on the basis of leaf characters. In fact, there are several different leaf types represented in this genus. The trichome complements are consistent, however, across most of the genus. None of the species bears tufts and nearly all are supplied with large, often resinous, globular to peltate trichomes. Short conical trichomes are also much more abundant in *Nothofagus* than in any genus of the Fagaceae sensu stricto. In spite of these common features, the leaf architecture is quite variable and few features characterize the genus as a whole. Because of this variability I differentiated four general leaf groups, each with a fairly distinct assemblage of characteristics that allows it to be distinguished from other groups of *Nothofagus* as well as other genera and families (Jones, 1984). The first (type I) can be briefly characterized as being evergreen and entire-margined. The second (type II) is evergreen with well developed serrations. The third (type III) is a rather heterogeneous group that is composed of deciduous nonentire-margined leaves. The fourth (type IV) is evergreen, entire-margined, and lacks the typical trichome complement characteristic of the above groups. A list of the species studied that belong in each group is given in Text-Figure 2.

The diversity and distribution of *Nothofagus* has made it an attractive subject for investigation (see, for example, Langdon, 1947; Camus, 1951; van Steenis, 1953, 1971a, 1971b; Cookson & Pike, 1955; Soepadmo, 1972; Hanks & Fairbrothers, 1976; Philipson & Philipson, 1979; Romero, 1980; Ragonese, 1981; Humphries, 1981; Aguirre & Romero, 1982; Romero & Aguirre, 1982; Praglowski, 1982). The group has been variously subdivided on the basis of reproductive and vegetative features. The classification of van Steenis (1953) is generally accepted. This scheme is built, in part, on foliar features, and thus there is some correlation between it and the division by leaf types found in Jones (1984) (see Text-Fig. 2). Palynologists divide the genus into three groups based on pollen characteristics (i.e., 'menziesii,' 'fusca,' and 'brassi' types), but these too show considerable divergence from van Steenis's scheme. In the final analysis, *Nothofagus* appears to be a heterogeneous assemblage. There is little doubt they are all related, at least at the family level (see Nixon, 1982), but the affinities within this group are more obscure.

The intrageneric diversity is related to the phytogeographic distribution. Although restricted to the Southern Hemisphere, *Nothofagus* is fairly wide ranging with occurrences in temperate South America, Australia, Tasmania, and New Zealand as well as tropical New Britain, New Caledonia, and New Guinea. The tropical species form the most homogeneous and well defined group. This group collectively and exclusively possesses type I leaves with conduplicate vernation (Philipson & Philipson, 1979) as well as 'brassi' type pollen.[3] Species of this type also possesses bipartite cupules, a character that can be found, only rarely, outside this group. In addition, the wood of these tropical forms appears to be consistent in form and distinguishable from those of temperate species (Dadswell & Ingle, 1954).

The temperate forms do not possess such uniformity even within "reproductively isolated" floral regions. For instance, the *Nothofagus* of South America, New Zealand, and Australia all possess more than one leaf type as well as multiple types of vernation and pollen (Text-Fig. 2). Both deciduous and evergreen forms can also be found in all but New Zealand. The distribution of these characteristics implies the existence of multiple parallel evolutionary events in several

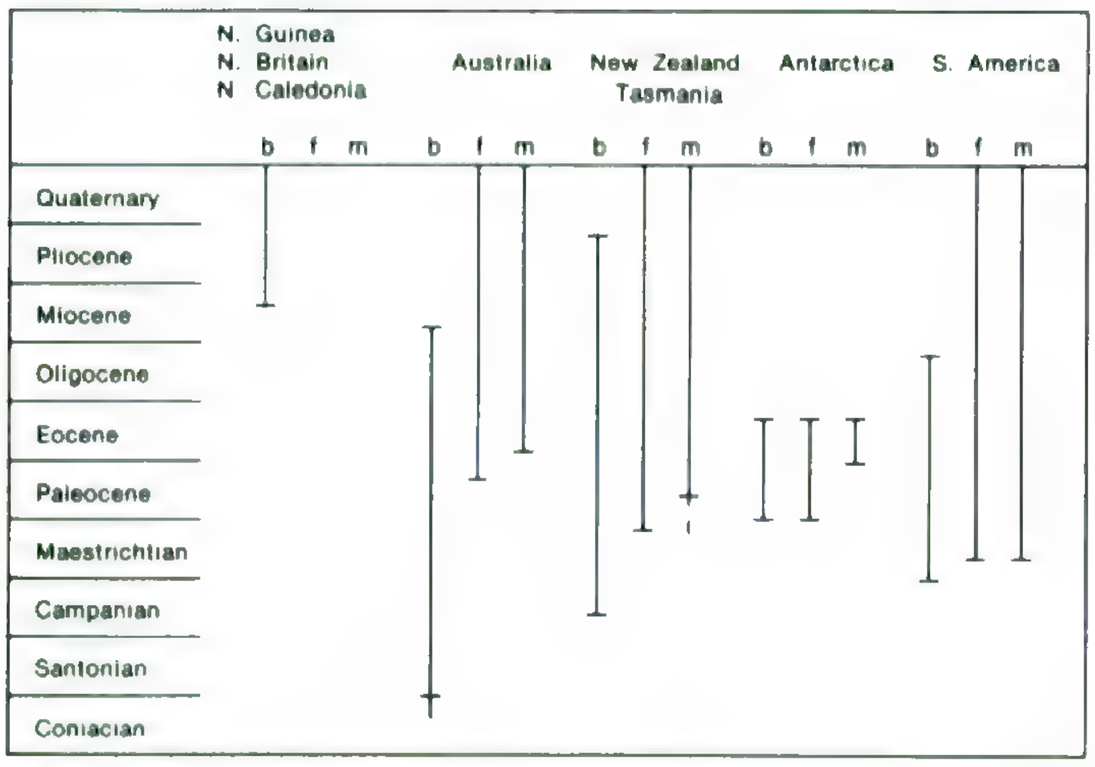
[3] Van Steenis (1971a) reported 'brassi' type pollen from *Nothofagus alessandrii*, a South American species that, according to Cranwell (1939), bears 'fusca' type pollen. Cranwell's assessment is probably correct. Praglowski (1982) as well as Hanks and Fairbrothers (1976) found 'brassi' pollen type to be exclusively associated with the tropical *Nothofagus* from New Guinea and New Caledonia.

Species	van Steenis section	Subsection	Habit	Vernation	Pollen	# Cupule parts	Geographical distribution
Leaf type I							
Nf. aequilateralis	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NC[2] (Trop.)
Nf. balansae	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NC (Trop.)
Nf. brassi	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NG[2] (Trop.)
Nf. codonandra	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NC (Trop.)
Nf. arenata	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NG (Trop.)
Nf. discoidea	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NC (Trop.)
Nf. grandis	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NG (Trop.)
Nf. pullei	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NG (Trop.)
Nf. rubra	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NC (Trop.)
Nf. starkenborghi	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NG (Trop.)
Leaf type II							
Nf. alessandri	Nothofagus	Antarcticae	d	Plicate	fusca	2(4)[1]	SAm[2] (Temp.)
Nf. alpina	Nothofagus	Antarcticae	d	Plicate	menziesii	4	SAm (Temp.)
Nf. antarctica	Nothofagus	Antarcticae	d	Plicate	fusca	4	SAm (Temp.)
Nf. glauca	Nothofagus	Antarcticae	d	Plicate		2(4)[1]	SAm (Temp.)
Nf. gunnii	Nothofagus	Antarcticae	d	Plicate	fusca	4	Tas[2] (Temp.)
Nf. obliqua	Nothofagus	Antarcticae	d	Plicate	menziesii	4	SAm (Temp.)
Nf. procera	Nothofagus	Antarcticae	d	Plicate	menziesii	4	SAm (Temp.)
Nf. pumilo	Nothofagus	Pumiliae	d	Plicate	fusca	4(2)[1]	SAm (Temp.)
Leaf type III							
Nf. betuloides	Calusparassus	Quadripartite	e	Plane	fusca	4	SAm (Temp.)
Nf. cunninghami	Calusparassus	Quadripartite	e	Plane	menziesii	4	Aust[2] (Temp.)
Nf. dombeyi	Calusparassus	Quadripartite	e	Plane	fusca	4	SAm (Temp.)
Nf. fusca	Calusparassus	Quadripartite	e	Revolute	fusca	4	NZ[2] (Temp.)
Nf. menziesii	Calusparassus	Quadripartite	e	Plane	menziesii	4	NZ (Temp.)
Nf. nitida	Calusparassus	Quadripartite	e	Plane	fusca	4	SAm (Temp.)
Nf. truncata	Calusparassus	Quadripartite	e	Revolute	fusca	4	NZ (Temp.)
Leaf type IV							
Nf. cliffortioides	Calusparassus	Tripartite	e	Revolute	fusca	3	NZ (Temp.)
Nf. solandri	Calusparassus	Tripartite	e	Revolute	fusca	3	NZ (Temp.)

TEXT-FIGURE 2. Comparison of proposed classification, by leaf type, with that of van Steenis (as reported in Soepadmo, 1972) and some individual properties of *Nothofagus* species. [1]Disparant values for this variable exist for these species, those in parentheses are from van Steenis (1953) and the others are from Philipson and Philipson (1979). [2]Aust = Australia, NC = New Caledonia, NG = New Guinea, NZ = New Zealand, SAm = South America, Tas = Tasmania.

character groups and/or the presence of the current diverse set of characters before reproductive isolation occurred (estimated by tectonic data to have been accomplished by the mid-Cretaceous; Smith and Briden, 1977).

Postulates based on plate tectonic information, such as that presented in Smith and Briden (1977), and biogeographic information do not conform to that from the fossil record. Tectonic data would indicate the existence of the ancestral group from which *Nothofagus* and other Fagaceae arose during the late Jurassic or early Cretaceous yet the earliest confirmed report of *Nothofagus* or any other Fagaceae does not occur until the Santonian (Muller, 1981) or perhaps Coniacian (Stover & Evans, 1973). This and all other Cretaceous reports of Fagaceae are based on pollen. The oldest record of *Nothofagus* (Dettmann & Playford, 1969) is from southern Australia. This pollen, *Nothofagidites senectus,* is of the 'brassi' type, which is the only type found until the middle to late Maestrichtian when the 'fusca' and 'menziesii' types appear simultaneously along with the 'brassi' type, in South America (Romero, 1973, 1977; Archangelsky & Romero, 1974; Menendez & Filice, 1975). The stratigraphic ranges of the pollen types in each major geographical region (Text-Fig. 3) imply a radiation of the 'brassi' type from southern Australia to South America and other points in its current range. The pollen record further suggests that the genus underwent considerable differentiation in or enroute to South America where the 'menziesii' and 'fusca' types first appear. These forms



TEXT-FIGURE 3. Distribution of *Nothofagus* pollen types (b = 'brassi'; f = 'fusca'; m = 'menziesii') through space and time; gaps are not shown. Modified and revised from Muller (1981) and Humphries (1981).

may have subsequently spread back across Antarctica to New Zealand and Australia. This hypothesis is highly conjectural at this point and must be tested along with a myriad of other hypotheses as we broaden the body of fossil evidence and determine, with greater accuracy, the stratigraphic position of previously reported forms. It should be noted that this and many other models require free routes of migration between South America and Australia at least into the Maestrichtian. Again, this is not in agreement with the current paleogeographic reconstructions. The cladistic representation of land mass separations constructed by Rosen (1978), however, indicates that sea boundaries were not formed until palynological differentiation, at least, had occurred. Van Steenis (1971a) circumvented discrepancies between the time of barrier formation and the emergence of various groups by suggesting the existence of some as yet unreported land bridges linking South America to Australia through Antarctica. Archipelagos or migrating microplates would account for the postulated migration. Schuster (1976) included reports of cordilleras that might satisfy van Steenis's requirements. The strength of biological evidence for the existence of free paths for dispersal supports either the existence of these discontinuous pathways or the later estimates for the separation of the "*Nothofagus*" province. If the earlier estimates of separation are accurate and van Steenis's land bridges did not exist, I would accept the occurrence of long distance transport, after the wide range of characters had evolved, rather than the multiple parallel evolutionary events that would be required to explain the current distribution of characters. Although unlikely, long distance dispersal may not be as irrational as it might first appear. It is true that an overwhelming body of evidence indicates that fruits of *Nothofagus,* and for that matter all extant Fagaceae, are not suited for long distance dispersal (Holloway, 1954; Cranwell, 1963, 1964; Preest, 1963). Yet, Tiffney (1984) has shown that substantial changes in fruit and seed sizes have occurred from mid-Cretaceous into the early Tertiary. The trends in size are undoubtedly correlated with changes in modes of dispersal and the evolution of various animal groups. Thus, the dispersal strategies exploited by fossil Fagaceae may have differed substantially from those of today. The presence of *Fagopsis,* a wind dispersed fagaceous plant from the Eocene and Oligocene of North America, underscores the need for flexibility when considering the dispersal mechanisms of fossil forms.

An intriguing phytogeographic problem is that of the center of origin and/or radiation. Postulated centers of origins include New Caledonia (Croizat, 1952), southeast Asia (Takhtajan, 1969), southeast Asia-Queensland (van Steenis, 1971a, 1971b), North America (Oliver, 1925; Schuster, 1976), Asia (Darlington, 1965), Northern Hemisphere (Raven & Axelrod, 1974) and "southern" (Couper, 1960a, 1960b; Cranwell, 1963). Although many postulate a northern origin, it is clear that most of the differentiation occurred in the Southern Hemisphere. A northern origin of *Nothofagus* (not a morphologically dissimilar ancestor) would likely leave a recognizable fossil record in that region. Although there have been several reports of *Nothofagus* or *Nothofagus* pollen from the Northern Hemisphere (Mtchedlishvili, 1961; Sein, 1961; Ames & Riegel, 1962; Kedves, 1964; Penny, 1969; Hopkins, 1969; Elsik, 1974), none provide convincing evidence for the existence of *Nothofagus* in that region. Pollen forms attributed to *Nothofagus* from the Maestrichtian of Siberia (Mtchedlishvili, 1961) and the Eocene London Clay (Sein, 1961) are said to be chloranthaceous (Kuprianova, 1967). She and others (e.g., Soepadmo, 1972) doubt the existence of *Nothofagus* in the Northern Hemisphere. Elsik (1974) refuted Kuprianova's assessment on the basis of exine sculptural differences between the fossil forms she studied and extant Chloranthaceae. It is interesting to note, however, that the pollen Elsik assigned to *Nothofagus* has an exine sculpture that is quite distinct from all living members of this genus.

As he tangentially suggested, this form may represent a fagaceous or pre-fagaceous ancestral form since the sculpturing is more like that found in extant *Fagus* and *Quercus* than in *Nothofagus*.

Megafossil evidence of *Nothofagus* is also lacking in the Northern Hemisphere. Bandulska (1923, 1924) reported *Nothofagus* leaves from the Eocene of Bournemouth, but her description of the leaf architecture was very brief and did not contain any information to indicate that the specimens under consideration were actually *Nothofagus*. She admirably included information and an illustration of cuticle from these leaves but again the description was very brief and the illustration did not show any characteristics that would confirm the generic affinities of this leaf type. The T pieces or "dagger-like" structures of which she spoke are common to many fagaceous genera and their presence in cuticle preparations is often related to leaf age and the length of maceration during cuticle preparation. Complex gland bases, common to nearly all *Nothofagus*, were not mentioned in the description and were not evident in the illustration. No subsequent reports confirming or augmenting her report have been made. There are other leaves from the Northern Hemisphere with architecture similar to those of *Nothofagus*. *Phyllites kryshtofovichii* (Klimova) Iljinskaja et Ablaev, for instance, has been compared to *Nothofagus moorei* (Takhtajan, 1982). No information on the cuticles of leaves such as these is available. Leaves of other members of the Hamamelidopsidae also possess the architectural characteristics of this and other similar leaf types, so until cuticular evidence is produced they cannot be considered as an indication of the presence of this genus in the Northern Hemisphere. There are no reports of wood, flowers, fruits, or other plant parts attributable to this genus from the Northern Hemisphere. A northern origin, for fully differentiated *Nothofagus*, therefore is unlikely. Raven and Axelrod's (1974) postulate that *Nothofagus* must have migrated to the Austral regions through Africa lacks corroborative fossil evidence. Raven and Axelrod (1974) recognized this deficiency, citing only two reports, one of which was attributed to contaminated drilling mud (Puri, 1965) and the other to windblown contaminants from South America (Schalke, 1973). Fossil evidence therefore strongly supports a southern origin for recognizable *Nothofagus*. This is not to say that a remote hamamelidopsid ancestor did not develop in the Northern Hemisphere and migrate to the south via Africa as suggested by Raven and Axelrod (1974) or North America as proposed by Oliver (1925).

The fossil record of *Nothofagus* is well represented in the Southern Hemisphere (e.g., Couper, 1953, 1960a, 1960b; Cookson, 1958; Cranwell, 1959, 1963; Romero, 1973; and many others). Pollen has been extensively studied and is found in the remnants of Gondwanaland except India, disregarding one questionable report from the Miocene (Ramanujam, 1966), and Africa (Axelrod & Raven, 1978). These two land masses were the first to become isolated during the fragmentation of Gondwanaland. Axelrod and Raven (1978) suggested that the evergreen southern beech–podocarp forests must have extended into southern Africa, but again they conceded that there is no fossil evidence to corroborate this assumption. Surely pollen evidence would have been found if this were the case. *Nothofagus* is known to produce massive amounts of pollen (van Steenis, 1971a; Soepadmo, 1972) and it often occurs as a dominant element in fossil assemblages. To me the absence of fossil forms on these continents argues for an origin in the Austral complex after the separation of these two land masses.

Megafossils are also abundant, yet they have been largely neglected. Fossil wood (*Nothofagoxylon* Gothan) has been described from the Upper Cretaceous or Tertiary (age uncertain) of Antarctica (Gothan, 1908) and the Oligocene to Miocene of southern South America (Kräusel, 1924; Cozzo, 1950; Boureau & Salard, 1960; Salard, 1961; Ragonese, 1977). The wood described is all of temperate type. Leaves are very abundant (Berry, 1938; Menendez, 1971) and have been described from Antarctica (Dusén, 1908; Orlando, 1964; Zastawniak, 1981), Australia (Ettingshausen, 1888), New Zealand (Ettingshausen, 1887a; Oliver, 1936), Tasmania (Hill, 1983a, 1983b), and South America (Dusén, 1899–1902; Frenguelli, 1941). Many of the leaf types described in the early literature were assigned to *Fagus* in accordance with the plant classification schemes for modern Fagaceae in vogue at that time. Although some leaf types do not appear to be *Nothofagus* or any other Fagaceae, most are comparable with *Nothofagus* on the basis of the information available. Except for Hill (1983a, 1983b), none of the studies provide cuticular information.

Considering the abundance of the leaf record and the early and widespread occurrence of the

'brassi' type pollen, one might expect to find entire-margined evergreen (type I) leaves in the fossil record, but this is not the case. Yet, the apparent absence of these leaves may be due to difficulties involved in identifying entire-margined leaves rather than a true absence. Cuticular material, when available, is a great asset when working with nondescript entire-margined leaves. Close examination of austral fossil floras may well reveal the presence of these *Nothofagus* forms.

All fossil *Nothofagus* leaf materials reported thus far have been from the Tertiary. The accuracy and precision of the age determinations are poor in most cases. Thus, at present, the leaf record can tell us little more than that deciduous and/or evergreen temperate (types II and III) *Nothofagus* were present in South America, Antarctica, New Zealand, and Australia during the Tertiary. A comprehensive review of fossil *Nothofagus* leaf forms is desperately needed.

The leaf architectural and cuticular morphology of extant *Nothofagus* has been the subject of several recent papers. Romero and co-workers (Romero, 1980; Aguirre & Romero, 1982; Romero & Aguirre, 1982) have surveyed the leaf architecture of nearly the entire genus, providing keys for the identification of leaves to the species level. Bandulska (1924) surveyed the cuticle of some *Nothofagus* and *Fagus* species, but her analysis was limited to only a few species and employed a restricted set of characters. Ragonese (1981), however, provided a much more complete analysis in her anatomical assessment of *Nothofagus* leaves, but she investigated only the South American forms. The results of Jones (1984) are in general agreement with those of the above studies.

Little can be said about intrageneric evolution on the basis of extant leaf characteristics alone. Romero (1980) stated that *Nothofagus antarctica* leaves were the most primitive among those of the South American species but did not provide foliar evidence to support this assertion. It seems he was echoing the assertions of van Steenis and others based on the presence of "primitive" reproductive features such as a two-parted cupule. Type IV leaves, characteristic of *N. solandri* and *N. truncata,* are specialized and do appear to be advanced. They possess a rather unique trichome complement that lacks large glands, common in the rest of the genus, and possess a dense cover of curly, thin-walled, solitary trichomes on the abaxial surface. This trichome type is restricted to this group with the exception of *Nothofagus glauca,* in which they are much less abundant and occur with thick-walled solitary trichomes and large glands. *Nothofagus gunnii* of Tasmania also lacks glands and possesses a rather distinct leaf architecture. This species may also represent a specialized form, but without corroborative fossil evidence we cannot know for sure. The often distinctive leaf architecture and rather unique cuticular characteristics should be of great value in the assessment of fossil *Nothofagus* leaf forms. The analysis of these forms will provide much valuable information about the evolutionary history of this important group particularly with regard to its origin and relationship to the Fagaceae sensu stricto and the Betulaceae.

CASTANEA MILL.

Castanea is a small genus of about 12 species, restricted to temperate regions of the Northern Hemisphere. It is a relatively homogeneous group showing little variability in leaf architecture and cuticular morphology. Reproductive and nonfoliar vegetative features (see, for example, Shimaji, 1962) also exhibit little variation in this genus. Unlike *Fagus,* however, this genus has been studied fairly thoroughly. Camus (1928–1929) presented a thorough monograph of the genus in which she adopted the subgeneric classification proposed by Dode (1908). According to this scheme, *Castanea* is divided into three sections, *Eucastanon, Balanocastanon,* and *Hypocastanon,* mainly on the basis of reproductive features (i.e., those of the fruit and cupule). Foliar characteristics provide some support for this classification. The leaves of section *Eucastanon,* for example, generally have more prominent teeth with distinct bristle tips. The uniseriate (type 15) and capitate (type 16) trichomes also have less prominent basal cells in species of this section. Capitate trichomes with multicellular heads are abundant in section *Eucastanon* whereas simple uniseriates are more abundant in the other two sections. The monotypic section *Hypocastanon* can be roughly distinguished from the other sections by the lack of abundant trichomes and subtle teeth, which often lack bristles. Some specimens of *C. henryi,* in fact, possess upturned setaceous tips. None of these features, however, can be relied upon to clearly differentiate subsections. The intraspecific variation, once again, meets or exceeds that between most species. Graves (unpubl. data) faced this problem in his

attempt to construct a key to the species of *Castanea* based on foliar features. He emphasized the variability of the foliar features and stressed the importance of relying on a number of characteristics rather than one or only a few. In the final analysis he was unable to construct a key to the species based entirely on foliar features. The variability is probably due, at least in part, to the reproductive properties of the group. Facile formation of hybrids is one of the salient characteristics of the Fagaceae, and *Castanea* is no exception. The formation of natural hybrids has long been noted and has caused the taxonomy, particularly of the "chinkapin" species, to be quite unsettled.

Castanea species are discontinuously distributed in temperate regions of the Northern Hemisphere. This group does not appear to compete as favorably in the cooler parts of the North temperate zone as *Fagus, Quercus,* and many other elements of the temperate forests. Fossil records indicate a typical "holarctic" distribution with records from Greenland (Heer, 1883), Alaska (Hollick, 1936), western North America (LaMotte, 1952), and other regions in which *Castanea* is no longer found. Since there is undisputed proof of the existence of *Castanea* (i.e., inflorescences, cupules, pollen, and leaves) by the Eocene (Crepet & Daghlian, 1980; Jones, 1984), the current distribution is in harmony with plate tectonic evidence.

Reports of castaneoid fossils span from the Santonian to the present. The first records are in the form of pollen. Castaneoid (Tricolpollenites type) pollen has been reported from the Lower Campanian of the Netherlands as well as the Santonian/Campanian of western Canada (Rouse et al., 1971). *Cupuliferites pusillus,* another taxon associated with the Castaneoideae, has been reported from the Maestrichtian of California (Chmura, 1973). Pollen corresponding to this type was later reported from Eocene *Castanea* inflorescences from southeastern North America (Crepet & Daghlian, 1980). Castaneoid pollen has been reported from the Upper Paleocene (Gruas-Cavagnetto, 1978) and Lower Eocene (Kedves, 1978) of Europe as well. Reports from the Eocene to the present abound (Muller, 1981). Palynological data alone cannot be used to indicate the presence of *Castanea* but rather only the Castaneoideae.

Wood resembling that of *Castanea* (i.e., *Castanoxylon* Navale) has been reported from the Neogene of Europe and Eocene-Miocene of India (Navale, 1964; Selmeier, 1970c; van der Burgh, 1978b). Wood, like pollen, is not generically specific in this group and similar wood is present in *Castanopsis* as well as some species of *Quercus* and *Lithocarpus* (Navale, 1964). *Castanea* flowers, which provide definitive proof, have been reported by Conwentz (1886) in the Eocene-Oligocene Baltic Amber and by Crepet and Daghlian (1980) from the Eocene of southeastern North America. There are very few reports of *Castanea* fruits in the fossil record. Kirchheimer (1957) listed only one doubtful occurrence (Beyn, 1940). Cupules have been found in the Eocene of southeastern North America (Crepet & Daghlian, 1980; Jones, 1984) but the only report of actual fruits is one of aborted fruits from the Pliocene of Germany (van der Burgh, 1978a). The rarity of *Castanea* as well as *Quercus* fruits in the fossil record is probably related to the lack of hard, durable ovary walls, or parts thereof, and the presence of abundant substrate for decomposer organisms. That the Pliocene fruits mentioned above were aborted fruits is consistent with this hypothesis. Most of the reproductive structures that were once assigned to *Castanea* are now considered to be *Castanopsis* (Kirchheimer, 1957), which is commonly reported from the Neogene of Europe.

The basic *Castanea* leaf form first appears during the Eocene in the form of *Dryophyllum tennesseense* (Jones, 1984). Similar leaves can be found in the Paleocene (e.g., Laurent, 1912; Crane, 1978), but few possess the regularity of secondaries and teeth characteristic of *Castanea* leaves, and those that do lack cuticle needed for identification. Many "castaneoid" leaf forms have been reported from the Eocene to the present (e.g., Nathorst, 1888; Berry, 1916; Knobloch, 1969; Takhtajan, 1982; Hummel, 1983). None of these leaves has been unquestionably associated with definitive reproductive materials, however, and similar forms can be found in other fagaceous and nonfagaceous genera. Many workers (e.g., Laurent & Marty, 1909; Ferguson, 1971) have specifically mentioned the difficulties involved when working with isolated *Castanea*-like leaves. The *Castanea*-like *Dryophyllum furcinervis* (Rossm.) Schmalh., for example, is thought by some to be *Castanopsis* (Kräusel & Weyland, 1950), whereas others hold it to be a distinct ancestral type (Raniecka-Bobrowska, 1962). Mai (1970) believed that the morphological and anatomical features are consistent with those of the genus *Trigonobalanus.* He further

suggested that these leaves are stratigraphically correlated with fossil fruits of this genus. Ferguson (1971) chose to leave it in the genus *Quercus* as suggested by Heer. Realistically, this leaf type could belong to this or to one of many other extant genera to which it has been assigned. It could just as easily represent an extinct form whether ancestral or not.

The foliar features of *Castanea* species do not provide any hint as to possible primitive forms within the genus. It may be possible to infer the primitiveness on the basis of correlated fruit and other features but even this would be tenuous when one considers the relative plasticity of leaf characters and the interspecific mixes characteristic of this taxon.

CHRYSOLEPIS HELMQV.

Chrysolepis consists of two sympatric species native to the Pacific western United States. This genus is recognized by many, but not all, prominent students of the Fagaceae (Hjelmqvist, 1948; Hutchinson, 1967; Forman, 1966b; Elias, 1971; Abbe, 1974). Others, Soepadmo (1972) for example, do not feel that the *Chrysolepis* species are sufficiently distinct to warrant separation from *Castanopsis*. In a communication to van Steenis, Soepadmo allegedly stated that if *Chrysolepis* is recognized as a separate genus at least one species from southeast Asia would have to be included (van Steenis, 1971a). Lawrence (1951) and Melchior (1964) did not recognize this genus but failed to support their position. Brett (1964) evidently did not recognize *Chrysolepis,* which is not too surprising since he also favored the fusion of *Castanopsis* and *Lithocarpus,* thus reducing the Castaneoideae to two genera.

Separation of *Chrysolepis* from *Castanopsis* is based primarily on differences in cupule structure (Forman, 1966b). Most of the other reproductive and vegetative features are similar if not identical. Erdtman (1943) for example, found the pollen of *Chrysolepis* (*Castanopsis*) *chrysophylla* to be indistinguishable from that of *Castanopsis* and *Castanea*. This has been supported recently using scanning electron microscopy (Crepet & Daghlian, 1980). The leaves of *Chrysolepis* and *Castanopsis* species are also very similar in gross form, venation, and cuticular characteristics. There are some differences, however, that can be employed to support the generic distinction. *Chrysolepis* leaves are generally smaller and somewhat xerophytically modified. Most tend to be elliptical to oblong rather than lanceolate as in most *Castanopsis*. The most consistent difference is in the trichome complement. Even these are similar, but both species of *Chrysolepis* possess thick-walled peltate trichomes with radially aligned cap cells (type 11, see Appendix III), which are totally lacking in *Castanopsis* species. Similar peltate trichomes are found in other Castaneoideae (i.e., *Castanopsis* and *Lithocarpus*) but these trichomes (type 13) have very thin collapsible cell walls, and the cap is composed of nonradially aligned cells. The taxonomic significance of these differences can be debated, but they do allow one to distinguish *Chrysolepis* leaves from those of other genera. I believe *Chrysolepis,* although very closely related to *Castanopsis,* should be recognized at the generic level.

The phytogeograpy of *Chrysolepis* can be interpreted in two different ways depending on the basic assumptions made about the group. Neither of these can be confirmed or rejected with the data currently available. If the genus is an ancestral form not derived from or closely associated with *Castanopsis,* as suggested by Elias (1971), it simply has a very restricted relict distribution. Yet, if *Chrysolepis* species are closely allied derived forms, perhaps even congeneric with those of *Castanopsis,* which are restricted today to southeast Asia and surrounding islands, the disjunction must be explained by one or more of the following: 1) long distance dispersal, 2) a widespread ("holarctic") past distribution, and 3) plate tectonic anomalies (i.e., rafting on microplates). Long distance dispersal is generally ruled out because of the current dispersal strategies adopted by this and other groups of extant Fagaceae. In contrast, the fossil record indicates that the range of *Castanopsis* was indeed much greater in the past. There have been reports of *Castanopsis* in western North America, Asia, and Europe (Kräusel & Weyland, 1950; LaMotte, 1952; Kirchheimer, 1957; Takhtajan, 1982). If these reports are accurate they, collectively, indicate a near pan north temperate distribution for *Castanopsis*. The absence of reports from eastern North America and other portions of the north temperate zone may be more a function of biases in the identification of fossil leaves than true distributional gaps. Leaves, which are the bases for most of the reports, are mostly entire-margined in *Castanopsis*. They are difficult if not impossible to distinguish from a host of other entire- and nearly entire-margined forms on the basis of leaf architecture alone. Thus, when ana-

lyzing leaves using only leaf form and architecture, one could quite likely assign *Castanopsis* leaves to other taxa with similar leaves particularly when encountered in regions where *Castanopsis* leaves are not expected. One only has to examine the synonymy lists in LaMotte (1952) to recognize the taxonomic diversity of forms that resemble *Castanopsis*. Cuticular features are very valuable in distinguishing forms with similar leaf architecture, yet, they are often neglected even when cuticle is preserved. Regardless of whether or not these gaps in the distribution are filled, the reports that exist indicate a sufficiently wide distribution of *Castanopsis* to account for the presence of *Chrysolepis* in its present range.

Although the current distribution is easily explained on the basis of paleoenvironmental information and the movement of large continental plates, some workers have suggested that western North American–southeast Asian disjuncts may have arisen by rafting on microplates such as those that form the southern portions of Alaska. Such explanations need not be invoked in this case, and little evidence for rafting has been presented.

The fossil record of *Chrysolepis* is scanty. Since the pollen of all Castaneoideae are similar, the earliest records may range back to the Santonian-Campanian (Muller, 1981). Reports from California (Chmura, 1973) and western Canada (Rouse et al., 1971) indicate castaneoid pollen was present in and near the current range of *Chrysolepis* by the late Cretaceous. *Chrysolepis* leaves (*Castanopsis chrysophylloides* Lesq.) have been reported from the Eocene to Pliocene (LaMotte, 1952). Dorf (1938) reported a leaf form, which he believed was most closely related to *Chrysolepis* (*Castanopsis*) *sempervirens,* but this report, like all other reports of species assigned to this genus, is based on gross form and architecture alone. Some of these reports, particularly those of Upper Miocene and Pliocene forms, are reasonable, yet cupules, upon which definitive identification must rest, have not been found. Because of uncertainty in generic identification it is impossible to tell, with the information available, precisely when *Chrysolepis* first evolved. If, as Elias (1971) suggested, this is an ancestral form, we might expect it to have evolved very early in the history of the family. It might account, at least in part, for the early reports of castaneoid pollen. However, if it is an advanced offshoot of *Castanopsis* (Brett, 1964) that evolved independently only after geological and environmental factors created reproductive isolation would we expect a post-Eocene, probably late Oligocene or early Miocene, origin. At present both an early origin, that is, Upper Cretaceous or Paleogene, and a late origin, that is, Neogene, seem equally plausible.

CASTANOPSIS (D. DON) SPACH.

Castanopsis is a fairly large genus estimated to contain from "approximately 30 species or more" (Hutchinson, 1967; Abbe, 1974) to about 120 species (Camus, 1928–1929; Forman, 1966b; Willis, 1973). The actual number of species is probably around 100, extrapolating from recent revisions (Soepadmo, 1972) of the Malaysian species. The lower estimates appear to come from nineteenth century works and/or the works of Soepadmo on Malaysian *Castanopsis.* The great variation in the estimated size of this genus is, in part, an indication that few have studied *Castanopsis* in its entirety. The only modern comprehensive treatment of the genus is that of Camus (1928–1929). Soepadmo (1968a, 1972) provided a more up to date treatment, but it is restricted to the Malaysian species and is not nearly as thorough as that of Camus. There are numerous, less comprehensive assessments included in papers dealing with the systematics of the Fagaceae in general, but these do not contain much information on foliar features.

Oersted (1871) and Camus (1928–1929) divided *Castanopsis* species into groups. Oersted (1871) absorbed the species of *Castanopsis* into *Castanea,* segregating them into three groups on the basis of foliar and reproductive features. Two groups were placed in the subgenus *Castanopsis,* within which he placed *Castanopsis* (*Castanea*) *indica* A. DC. ex Seem., a species with acute serrate leaves, in one section and those species with entire or paucidentate leaves in a second. The remainder of the *Castanopsis* species were segregated in a second subgenus, *Callaeocarpus* (Miq.) Oersted. De Candolle (1868) separated the species of *Castanopsis* in a similar fashion but held this genus to be distinct from *Castanea.* Camus (1928–1929) divided the species of this genus into three sections using only reproductive features. Unfortunately, there are no foliar features that can be used to clearly distinguish these three sections.

The degree of variation in the leaf architectural and cuticular features of *Castanopsis* leaves varies considerably. The margins, for example, range

from entire to completely serrate. The venation varies similarly from camptodromous to craspedodromous. The fine venation is fairly consistent within the group except as modified by gross architectural differences. There is some variability in the cuticle as well but nearly all have a rather distinct speckled appearance. The serrate forms tend to possess tufts (type 5 trichomes, see Appendix III), which are otherwise rare in this genus. Nearly all species possess thin-walled peltate to "stellate" (type 13) trichomes abundantly distributed over the lower epidermis. These trichomes often cover the lower surface and obscure other epidermal features. It is the bases of these trichomes that give *Castanopsis* cuticles their characteristic speckled appearance. This trichome type allows one to distinguish *Castanopsis* leaves from most other tropical fagaceous leaves. It does occur in a few *Lithocarpus* species though, making absolute determinations of these leaves impossible at the generic level. Similar trichome forms occur in *Trigonobalanus doichangensis* (type 19) and *Chrysolepis* (type 11), but these can be distinguished readily from those of *Castanopsis*.

In spite of the variability in foliar features within the entire genus, most species of *Castanopsis* bear leaves of a single general type. The basic form of these leaves is similar to those of mesic tropical species in other fagaceous genera. The abundance of this generalized leaf type in *Castanopsis* is probably due, in part, to the rather limited geographic distribution of this genus.

Castanopsis is native only in southeast Asia, Indonesia, Korea, and Japan but the phytogeographic distribution is reputed to have been much wider in the past (Soepadmo, 1972). Kirchheimer (1957) suggested that fruits assigned to *Castanopsis salinarum* (Unger) Kirchheimer from the Oligocene of Europe are definitively *Castanopsis*. Many others have reported *Castanopsis* fruits, leaves, and/or wood from the middle to late Tertiary of Europe (e.g., Notzold, 1961; Szafer, 1961; Raniecka-Babrowska, 1962; Mai, 1964; Selmeier, 1970a, 1970b, 1972; Jung et al., 1971; van der Burgh, 1973). Ogura (1949) has reported wood of this genus from Japan, and Takhtajan (1982) included a number of *Castanopsis* leaf forms from eastern Europe and Asia. Wolfe (1968) reported a new species of *Castanopsis* from the Eocene of North America and further suggested (1973) that leaf material (i.e., that of MacGinitie, 1941) is truly *Castanopsis* (non *Chrysolepis* Hjelm.). Dorf (1938) reported a *Castanopsis*-like form, which he believed to be *Castanopsis* sensu stricto from the Tertiary of Idaho. *Chrysolepis* forms are also present in western North America (Axelrod, 1944; Chaney, 1944). Yet, these North American reports, those in Takhtajan (1982), and most others dealing with leaf material fail to give any information on the cuticle of the fossils in question. Even with cuticle, the leaves of this genus are often indistinguishable from some species of *Lithocarpus* and *Quercus* (see for instance Forman, 1964a, 1966a, 1966b). Therefore, fossil forms cannot be assigned at the generic level with certainty. Kräusel and Weyland (1950) were the first to use cuticular features to classify material as *Castanopsis*, but few have utilized these important features since. There are no reports of fossil *Castanopsis* fruits, or other reproductive macrofossils, in either North America or Asia to corroborate questionable leaf data.

There are no credible megafossil records of *Castanopsis* prior to the Eocene. Yet, pollen comparable to that of *Castanopsis* has been reported as early as the Upper Cretaceous (Santonian/Campanian of Canada; Rouse et al., 1971). *Castanopsis*-like pollen has also been reported from the Eocene of Great Britain (Chandler, 1964) and Europe (Kedves, 1978). Reports of *Castanopsis*-like pollen are, in fact, quite common throughout the Northern Hemisphere since the Eocene (Muller, 1981). As previously mentioned, however, the pollen of *Castanopsis* is not distinct but rather belongs to a generalized "castaneoid" type. Therefore, the presence of this pollen type does not necessarily indicate the presence of *Castanopsis*.

The fossil record can be interpreted as indicating an origin perhaps as early as the Upper Cretaceous but more likely in the early Tertiary. This genus was apparently widely distributed during the Eocene to Miocene and was lost in North America, Europe, and most of Asia during the Pliocene. Modern phylogenies suggest a fairly long evolutionary history for this genus, but forms included by the modern circumscription of *Castanopsis* are not generally considered to be primitive within the family.

The foliar features of this genus do not appear to be particularly advanced or primitive. The peltate (type 13) trichomes seem, intuitively, to be somewhat advanced yet the speckled appearance, lent by the bases of these trichomes, is present in some early forms of *Dryophyllum* and similar leaf types (Jones, 1984). Although the

foliar characteristics do not tell us much about the evolutionary status of this group within the family, they do support the separation of *Castanea* from *Castanopsis,* instead of the union suggested by Oersted (1871) and Brett (1964). In addition to morphological differences indicated by other authors (e.g., Camus, 1928–1929; Forman, 1964a, 1966a, 1966b), *Castanea* species do not possess the peltate trichomes characteristic of *Castanopsis* but rather bear capitate trichomes and tufts that are rare or absent in extant *Castanopsis.*

LITHOCARPUS BLUME

Lithocarpus is a large complex genus estimated, by some, to contain about 300 species (Willis, 1973). It has been split into two or more genera by several investigators (Oersted, 1871; Schwarz, 1936a; Nakai, 1939; Masamune & Tomiya, 1948; Brett, 1964). Others have distributed "*Lithocarpus*" species among sections of the genus *Quercus* (de Candolle, 1868). Camus (1934–1954), Forman (1964a, 1964b), and Soepadmo (1970, 1972) suggested that there was no basis for splitting this taxon. The boundaries between *Lithocarpus, Castanopsis,* and *Quercus* have long been a subject of controversy. Modern workers agree that *Quercus* and *Lithocarpus* are phylogenetically distinct, even though they show many parallel traits (Brett, 1964; Forman, 1964a, 1966a; Soepadmo, 1970, 1972). Luong (1965) and Forman (1966b) further suggested that *Castanopsis* and *Lithocarpus* can be clearly separated, at least phylogenetically, using specific vegetative and reproductive features. It is clear, however, that considerable mosaic and parallel evolution has occurred in this family.

There is little correlation between foliar features and most intrageneric classification schemes, which are based primarily on cupule morphology and other reproductive features. For example, very few of Camus' 14 subgenera are distinct and homogeneous with respect to foliar features. *Lithocarpus* leaves, in general, show relatively little variability. They are usually entire or only partly toothed. Only *L. densiflorus* has strongly serrate margins and then only in a few forms (e.g., *L. densiflorus* forma *attenuato-dentatus,* Tucker et al., 1969). Leaves of *Lithocarpus* are persistent to tardily deciduous. The basic leaf form is, in fact, very similar to those of other tropical fagaceous genera (i.e., *Castanopsis* and *Quercus* particularly those of the subgenus *Cyclobalanopsis*). Fortunately, most leaves of this genus can be distinguished from those of other genera using epidermal features. Appressed laterally attached (type 9, see Appendix III) trichomes are present in nearly all *Lithocarpus* species, and it is interesting to note that recent revisions (Soepadmo, 1970, 1972) involve the transfer of many species lacking this trichome type to *Castanopsis* and *Quercus.* As the taxonomy of *Lithocarpus* is further refined, this character may approach perfect agreement with those that are definitive.

The relative uniformity of *Lithocarpus* foliar features is probably a function of its rather limited distribution. With the exception of *L. densiflorus,* this genus is restricted to southeast Asia, Indonesia, and southern Japan. *Lithocarpus densiflorus,* which is found only in the Pacific southwestern part of North America, has rather distinctive foliar characteristics. Leaves of this species lack acuminate tips as well as other features common to the tropical oriental species of this genus. These sclerophyllous leaves invariably lack the appressed laterally attached (type 9) trichomes, common to most *Lithocarpus* species, and possess unique multiradiate (type 10) trichomes. The differences between the leaves of this species and those of the eastern species suggest rather distant affinities. Forman (1964a, 1964b, 1966a, 1966b; pers. comm., 1980) and others (e.g., Soepadmo, 1972) indicated, however, that the reproductive and nonfoliar vegetative features clearly associate this species with *Lithocarpus.* Although *L. densiflorus* may fit within *Lithocarpus,* the disparity in the foliar characteristics suggests a significant period of reproductive isolation in dissimilar environments.

The presence of *Lithocarpus* on both sides of the Pacific Ocean implies that this genus had a more extensive range in the past that must have bridged Asia and North America. Thus fossil *Lithocarpus* might be expected to occur at high northern latitudes on both continents. One might also assume that the distribution would extend to Europe as well since this is a pattern common to many contemporary floral elements. Yet, reports of this genus from the Northern Hemisphere are extremely rare. LaMotte (1952) listed only one North American species, *L. klamathensis* (MacGinitie) Axelrod, which occurs in the Miocene and Pliocene of the Pacific Northwest. Axelrod (1966) subsequently reported *Lithocarpus* leaves and a cupule from the Eocene (age uncertain) of Nevada. Axelrod and Raven

(1978) suggested that Miocene *Lithocarpus* gave rise to forms of *L. densiflorus* that occur in California today. Cuticular information, currently unavailable, should help to clarify the affinities of these fossil leaves.

Reports are equally rare from Europe. Saporta and Marion (1878) established the genus *Pasaniopsis* to contain *Pasania* (*Lithocarpus*)-like fossil leaves from the Paleocene Gelinden Flora. Only leaf architectural information is given for this material. It is consistent with placement near *Lithocarpus,* but cuticular information is needed before this leaf type can be allied to this genus with confidence. Andreánsky (1966) reported "undoubted" *Lithocarpus* from the Oligocene of Hungary. Yet, the published description and figures do not reveal a basis for this assignment. Only two probable fossil *Lithocarpus* species have been reported from Asia (Takhtajan, 1982). These two leaf forms are from Kazakhstan, and their ages were not reported. The figures of these leaf types reveal intersecondary veins and biconcave teeth that are not characteristic of *Lithocarpus* leaves. It is unlikely that these leaf forms belong to this genus.

The pollen of *Lithocarpus,* as previously mentioned, is of a generalized type and cannot be distinguished from other castaneoidean forms. Records of this pollen type, however, are common throughout the Northern Hemisphere. The first records of this type of pollen are from the Upper Cretaceous (Santonian/Campanian) of Canada (Rouse et al., 1971). No additional reports of wood, fruits, flowers, or other fossil materials have been made.

The paucity of fossil *Lithocarpus* in present North Temperate zones may be a function of difficulties in the identification of isolated organs of this genus rather than a true absence. MacGinitie (1969) acknowledged these difficulties when describing a leaf form from the Eocene Green River Flora. He contended, however, that suitable distinctions could be made in most cases if fourth order venation was available. Unfortunately, he did not mention the specific characteristics with which these distinctions can be made. I did not observe any reliable differences in the higher order venation of these genera.

Foliar features generally confirm the integrity of the genus as it has been recently circumscribed (Camus, 1934–1954; modified by Soepadmo, 1970, 1972). However, they do support the distinction of *Limlia* as suggested by Masamune and Tomiya (1948) on other grounds. The features upon which this genus was originally based seem rather weak and when considered alone would not, in my opinion, justify separation at the generic level. However, *Limlia* leaves are distinct from those of nearly all *Lithocarpus* in that they lack type 9 trichomes and possess a dense coat of type 13 trichomes as in *Castanopsis.* Interestingly, additional work on wood anatomy (Lee, 1968) has shown that the closest affinities of the species in question lie with *Castanea* and *Castanopsis* rather than *Lithocarpus.* This is consistent with the aforementioned leaf data. Hence, the recognition of this somewhat intermediate taxon at the generic level may be warranted. The same epidermal characteristics support the retention of the *Castanopsis fissa*-group in *Castanopsis* rather than inclusion in *Lithocarpus* as suggested by Camus (1934–1954).

Finally, the significance of the foliar features of *Lithocarpus densiflorus* deserves consideration. The presence of a unique trichome complement and distinctive leaf architecture sets this species apart from all other *Lithocarpus.* Foliar features would provide very strong support for generic distinction if other, more definitive, features so indicated. The intraspecific variability in foliar characteristics would also support recognition of some varieties as separate species (e.g., *L. densiflorus* var. *echinoides*).

TRIGONOBALANUS FORMAN

The genus *Trigonobalanus* was established in 1962 by Forman with a complement of one species, *T. verticillata,* and was expanded to two species, with the reassignment of *Q. doichangensis* Camus, in Forman's detailed description of the genus (1964a). Lozano-C. et al. (1979) further expanded the genus to three species as the result of the discovery of *T. excelsa* in South America. The small size and proposed primitive position of this taxon (see Forman, 1964a) has made it an attractive subject for investigation (see Forman, 1962, 1964a, 1966a; Cutler, 1964; Erdtman, 1967; Forman & Cutler, 1967; Hou, 1971; Soepadmo, 1972; Lozano-C. et al., 1979; Mennega, 1980; Hernández-Comacho et al., 1980; Baas, 1982). This genus has been assigned to various subfamilies (Forman, 1964a, 1964b; Melchior, 1964; Lozano-C. et al., 1979) but has not been formally subdivided above the species level. *Trigonobalanus,* small as it may be, does show considerable intrageneric variation. Erdtman (1967) for example, felt that the pollen mor-

phology of *T. doichangensis* and *T. verticillata* differed sufficiently that inclusion in separate sections or even separate genera should be considered. Mennega (1980) found substantial differences between the wood anatomy of these two species as well but felt that they were congeneric and closest to the Quercoideae. The male inflorescences of *Trigonobalanus* species vary as well, ranging from rigid, as in the Castaneoideae, to flexuous, as in most Quercoideae.

The leaves of *Trigonobalanus* also exhibit major differences. *Trigonobalanus verticillata,* for example, possesses whorled leaves, a characteristic unique to this species within the Fagaceae. The leaves of all *Trigonobalanus* species are similar in form to those of many other tropical Fagaceae (i.e., some *Castanopsis, Lithocarpus,* and *Quercus*). All species possess entire or mostly entire leaves of similar gross form. *Trigonobalanus doichangensis,* however, has leaves that are distinct from the other two species in that they are invariably entire and possess cuticles bearing papillae and rather exotic multicellular "peltate" (type 19) trichomes. Baas (1982) correctly concluded that *T. doichangensis* is an outlier with respect to leaf anatomy. In fact, the leaves of *T. excelsa* (of South America) and *T. verticillata* (of Malaysia) share many more common foliar features than either do with *T. doichangensis* (of Thailand). In spite of substantial intrageneric variability, leaf architectural and cuticular features together still allow leaves of *Trigonobalanus* species to be distinguished from other tropical Fagaceae (see Appendix II).

The intrageneric variability is undoubtedly related to the wide "disjunct" distribution of this taxon. *Trigonobalanus* is found in Thailand, the Malay Peninsula, Borneo, Celebes, and in Colombia, South America. These ranges may well be extended in the future since the genus is so new and many of the areas in which it might likely be found are poorly explored. The known range of this genus is quite wide but patchy, suggesting it is a relict of a much broader past distribution. A once broad distribution is almost demanded in order to account for the present occurrences. The range of *Quercus,* although more extensive today, is quite similar to that of *Trigonobalanus.* Both were probably circumboreal in the past. *Trigonobalanus* probably entered South America during the Miocene along with *Quercus.* Neither genus has penetrated past Colombia in South America. Unlike *Quercus, Trigonobalanus* seems to have become extinct in temperate regions, perhaps due to intolerance of the late Tertiary climatic deterioration. We must turn to the fossil record to confirm the presence or absence of this genus in higher latitudes of the Northern Hemisphere.

The fossil record of *Trigonobalanus* is very scanty. There are no confirmed reports of fossil *Trigonobalanus* pollen although it is very similar to that of *Quercus* and therefore may have been assigned to typical quercoid form genera. No *Trigonobalanus* wood, flowers, or fruits have been confirmed but paleogene reproductive materials under investigation by W. L. Crepet and S. R. Manchester may prove to be from plants of this genus. In addition, Forman (1964b) has suggested that the fossil fruits assigned to *Fagus succinea* Goeppert & Menge are quite similar to those of this genus. Mai (1970) assigned four fruit types from the Eocene and Miocene of Europe to *Trigonobalanus.* Forman (pers. comm., 1980) suggested that some of the types probably represent *Fagus* and others, although possibly *Trigonobalanus,* cannot be assigned to this genus with certainty using available information. Mai (1970) also suggested that these fruits were correlated with *Castanea*-like leaves previously assigned to *Dryophyllum furcinervis* Schmalhausen. The leaves have been placed in several genera including *Phyllites, Castanea, Quercus,* and *Castanopsis* (Kräusel & Weyland, 1950). The cuticle, as illustrated by Kräusel and Weyland (1950), indicates that the leaves probably do not represent *Castanea.* The trichome bases are scattered and simple, resembling those of *Castanopsis.* Mai (1970) correctly suggested that the epidermis is also similar to that of *T. doichangensis.* Yet, the leaf architecture is much more similar to extant members of the Castaneoideae than to those of extant *Trigonobalanus.* The nature of the trichomes themselves, when known, will probably shed some light on the affinities of this leaf type. The reports of *Trigonobalanus* (Mai, 1970; Gregor, 1980; Takhtajan, 1982), if correct, would support the hypothesis of a Laurasian distribution during the Tertiary. We still do not have any significant indication that *Trigonobalanus* was present in North America. A search for this genus in the fossil record of this continent is in order.

Trigonobalanus must have evolved prior to the Eocene (most likely in the latest Cretaceous or Paleocene) if it is an ancestral form within the Quercoideae (see Forman, 1964a, 1966a; Elias, 1971). If *Trigonobalanus* evolved from a casta-

neoid ancestor, as Forman (1966a) and Elias (1971) imply on the basis of cupule characteristics, and if the cupule characteristics are linked to foliar characteristics, we might assume that leaves of the most primitive *Trigonobalanus* would most closely resemble those of the supposed ancestors (i.e., near *Chrysolepis,* Elias, 1971). If these assumptions are correct, *Trigonobalanus doichangensis* would be the most primitive species in this genus. This species possesses entire leaves and multicellular branched trichomes that sometimes resemble the scales of *Castanopsis.* This hardly seems to be the case however, since this species is more advanced with regard to reproductive features that are usually considered to be more conservative (i.e., flexible male catkins and cupules usually bearing a single fruit). However, the scale-like trichomes may be derived, as they appear to be based on trichome data alone. We must remember that the evolutionary rates and even directions of various organs and characters can differ. Thus, primitive foliar characters cannot be determined with certainty using information gathered from extant species alone. It seems advisable to wait for further information on the nature of fossil forms before making firm conclusions about evolutionary trends in leaf characteristics of this group.

QUERCUS L.

Quercus is the largest genus in the Fagaceae, with an estimated 300 (Lawrence, 1951; Elias, 1971) to 600 (Soepadmo, 1972) species. This genus has been studied often, but, because of its immense size and wide distribution, few have studied the genus in its entirety. Camus (1934–1954) has comprehensively monographed the genus in three monumental volumes. Although some disagree with finer points of her classification scheme, most modern taxonomists generally accept Camus' circumscription of the genus. Historically, however, the circumscription of the genus has been highly controversial. Some have suggested that it is heterogeneous enough that it should be divided into two or more genera. Schottky (1912), Hjelmqvist (1948), Brett (1964), and others, for example, recognized Camus' subgenus *Cyclobalanopsis,* as a separate genus. Schwarz (1936a) went so far as to divide *Quercus* into four separate genera. A significant number of taxonomists accept the recognition of *Cyclobalanopsis* (e.g., Hsu & Jen, 1979) but few support the extensive splitting proposed by Schwarz (see, for example, Muller, 1942a). In contrast, many have suggested that *Quercus* should be united with morphologically similar *Lithocarpus* (e.g., de Candolle, 1868; Bentham & Hooker, 1880; Corner, 1939). Most modern workers (e.g., Camus, 1934–1954; Forman, 1964a, 1966a; Melchior, 1964; Soepadmo, 1968b, 1972) have suggested that there is a clear basis for distinguishing these as two genera. This certainly seems to be the case from a palynological point of view, but the intrageneric variability and extensive parallelism in wood, leaves, fruits, and other features often make discrimination difficult without detailed examination of fertile material.

Foliar variation in *Quercus* is not tightly correlated with established major infrageneric classification. Leaves of the subgenus *Cyclobalanopsis* (sensu Camus, 1934–1954) can be separated from those of the subgenus *Euquercus,* but there is considerable overlap among the sections of the latter. The sections often can be differentiated in a particular geographical area (Trelease, 1924; Dyal, 1936; Muller, 1942b; Barnett, 1944), but the distinctions become obscure when species from other geographical areas are considered. Numerous examples of parallel and convergent evolution of leaf forms have been noted in this genus (Tucker, 1974). Foliar variation in *Quercus* seems to be more closely associated with phytogeographic and environmental factors than with the definitive reproductive features that are the basis for classification at the section level.

Quercus has the widest distribution of all fagaceous genera. Its species are found in nearly all north temperate forests and woodlands, often as dominant elements. They are also abundant in subtropical and tropical regions of the Northern Hemisphere extending into the Southern Hemisphere only in northern South America and Indonesia. The wide geographical distribution probably accounts, at least in part, for the large variation in leaf form observed within *Quercus.* Brenner (1902) noted correlations between many foliar features and the geographical origin of the specimens. He also experimentally demonstrated substantial intraspecific effects of the environment on leaf form.

There is more foliar variability in this genus than in any other genus of Fagaceae. The leaves range from entire, nearly glabrous, tropical forms with drip tips and a coriaceous texture, to lobed, hairy, chartaceous forms characteristic of many temperate species. Camus (1934–1954) and others have noted the existence of specific leaf types

among *Quercus* species. There are entire-margined "laurel" and "willow" oaks, spiny sclerophyllous "holly" oaks, chartaceous "chestnut" oaks as well as typical lobed "white" and "red" oaks. Unfortunately, the types are not section specific, making classification at this level difficult when using leaf material alone (see Text-Fig. 4). Even trichome complements fail to allow clean separation of sections. This foliar variability often extends to lower taxonomic levels. The foliar variation within species is frequently dramatic, and foliar characteristics of species sometimes intergrade. Such intergradation is often the result of actual gene flow between species. The oaks are noted for their propensity toward hybridization (Trelease, 1917; Muller, 1942a, 1942b, 1952; Stebbins et al., 1947; Palmer, 1948; Bray, 1960; Benson, 1962; Hardin, 1975; Jensen & Eshbaugh, 1976), calling into question strict application of the biological species concept (Muller, 1942a; Burger, 1975; Crovello, 1976; van Valen, 1976). The capacity for genetic exchange may be one of the factors that makes the oaks very competitive in a wide range of environments.

General leaf type	Cyclobalanopsis	Euquercus					
		Cerris	Mesobalanus	Lepidobalanus	Macrobalanus	Protobalanus	Erythrobalanus
Entire or partially toothed, elliptical to lanceolate evergreen	•			•		•	•
Entire, broad tradily deciduous to evergreen				•			•
Xeromorphic, sclerophyllous, small, entire margined evergreen		•		•		•	
Sclerophyllous holly-like		•		•	•	•	•
Craspedodromous "chestnut"-like	(•)	•		•	•		(•)
Rounded coarsely toothed, deciduous			•				•
Roundly lobed deciduous		•	•	•			•
Sharply lobed deciduous		•		•			•

TEXT-FIGURE 4. Distribution of general leaf types among the subgenera and sections of *Quercus*.

The present broad distribution of *Quercus* is in harmony with the fossil record of this group. *Quercus,* like most fagaceous genera, had a "holarctic" distribution during the Neogene. There are abundant reports of fagaceous fossils from North America (see Trelease, 1918, 1924; LaMotte, 1952). These include reports of leaves (e.g., Lesquereux, 1878; Edwards, 1931; Chaney & Sanborn, 1933; Axelrod, 1956, 1964; Dorf, 1960, 1964; MacGinitie, 1969; Daghlian & Crepet, 1983; Manchester, 1983), wood (e.g., Platen, 1908; Schuster, 1908; Eames, 1910; Boeshore & Jump, 1938; Beyer, 1954; Prakash & Barghoorn, 1961a, 1961b; Wheeler et al., 1978), and reproductive materials including inflorescences (e.g., Daghlian & Crepet, 1983), nuts (e.g., Newberry, 1898; Manchester, 1981a, 1983), and cupules (e.g., Bones, 1979; Daghlian & Crepet, 1983; Manchester, 1983). *Quercus* remains are also abundant in Europe (Andreánsky & Kovacs-Sonkody, 1955; Kirchheimer, 1957). Leaves are reported most often (e.g., Schimper, 1870–1872; Kovacs, 1961; Andreánsky, 1966; Gazeau & Koeniguer, 1968; Sitar, 1974; Petrescu, 1976; Gros, 1983; Hummel, 1983), fruits (e.g., Heer, 1869; Saporta & Marion, 1878; Raniecka-Bobrowska, 1962; Hummel, 1983), cupules (e.g., Goeppert, 1855; Gregor, 1980; Hummel, 1983), and wood (Müller-Stoll & Madel, 1957; Brett, 1960; Selmeier, 1971; Prive, 1975), are also very common. Takhtajan (1982) listed and illustrated many *Quercus* leaves, woods, and reproductive materials from eastern Europe and Asia. Hu and Chaney (1940) reported *Quercus*-like leaves of the castaneoid type from the Oligocene to the Pliocene of China. More recent Chinese reports (Chinese Neogene Plant Editorial Group, 1978; Shuangxing, 1980) listed several fagaceous fossils including *Quercus* leaves from the Eocene. A large amount of work has been done on the Tertiary flora of Japan, and many species of *Quercus* and other fagaceous genera have been found (Nathorst, 1888; Tanai & Onoe, 1961; Chaney, 1963; Tanai & Suzuki, 1965; Matsuo, 1968; Tanai, 1970; Tanai & Yokoyama, 1975). *Quercus* has been reported also from various arctic and other high latitude localities (Heer, 1870, 1883; Hollick, 1936; Koch, 1963). It appears that *Quercus* is a recent immigrant to Africa for it is found only near the Mediterranean from the late Neogene to the present (Kräusel, 1939; Raven & Axelrod, 1974). There have also been reports from Australia and other Southern Hemisphere localities, beyond the current range (Ettingshausen, 1887a, 1887b, 1888; Krasser, 1903; Berry, 1923), but these appear to be in error. The fossil record of *Quercus* parallels that of many other north temperate arborescent forms. *Quercus* appears to have been an important part of the "Arcto-Tertiary" geoflora. During the course of the Tertiary, species of this group have migrated latitudinally in response to climatic conditions (see, for example, Tanai, 1961, 1967; Tanai & Huzioka,

1967), but they have maintained their ability to compete favorably with other broad-leaved forms. Unlike *Lithocarpus* and *Castanopsis, Quercus* has survived in Europe as well as Asia and across North America.

The time and place of the origin of *Quercus* is uncertain. Pollen of the *Quercus* type has not been found in sediments older than the Oligocene (Muller, 1981). Yet, many reports of Cretaceous leaves exist (e.g., *Quercophyllum chinkapinense,* Ward, 1905, Cenomanian). Most are poorly preserved and none have proven to be *Quercus.* Trelease (1918, 1924), although accepting the presence of *Quercus* in the Cretaceous, noted that many fossil leaves assigned to this genus are placed there for lack of a better place to put them. This is particularly true of the fossil leaf types he assigned to form groups that have no counterparts among modern *Quercus* (e.g., Fraxinifolae, Distinctae, and Suspectae). The tendency to assign fossil leaves to *Quercus* without solid morphological or anatomical evidence is probably a function of two intrinsic properties of the oaks. First, they are so widespread and abundant that oaks might be expected in almost any Northern Hemispheric arborescent angiosperm flora. Second, *Quercus* leaves are so variable that counterparts to many fossil leaf forms can be found among the highly variable and wide ranging leaf types found among modern members of this genus. The first believable, but still not conclusive, record of *Quercus* (Bones, 1979; Manchester, 1981a, 1983) is from the Middle Eocene Clarno Formation of Oregon. Leaves and wood, as well as nuts and cupules can be found here, strongly suggesting the presence of *Quercus* in fairly modern form at that time. Floral elements are needed to confirm the generic affinity, however, since the features found in the fossils are not definitive. Similar wood and fruits can be found, for example, in *Lithocarpus.* Crepet and Zavada (1983) have an inflorescence that is essentially like those of *Quercus* from the Middle Eocene Claiborne Formation (possibly Upper Paleocene–Lower Eocene Wilcox Formation; Zavada, pers. comm.) of Tennessee. The pollen, however, is different from that of typical *Quercus* pollen. The significance of the differences are currently being evaluated and may be developmentally rather than taxonomically related. It is likely that this will prove to be the earliest definitive evidence for the existence of *Quercus* or a close relative thereof. Flowers of this genus have been reported from the Eocene-Oligocene Catahoula Formation (Daghlian & Crepet, 1983). Based on this evidence we can say that *Quercus* was definitely present by the Oligocene and was probably present in the Eocene or perhaps earlier.

When the leaf record is examined, we find that the earliest apparently valid reports of *Quercus* are of entire- and serrate-margined forms. Brenner (1902) felt that the entire-margined forms were indeed the most primitive within the genus. There are lobed forms reported from the Cretaceous, but the nature of the leaves themselves does not provide convincing evidence of fagaceous affinity. In fact, they are most often closer to other extant families. The first plausible lobed oak is that reported by Daghlian and Crepet (1983) from the Oligocene. Lobed forms do not become common, however, until the Miocene (Tanai & Yokoyama, 1975). Rüffle and Knappe (1977) suggested that lobation in oaks is an atavistic phenomenon that recalls the palmately lobed nature of distant ancestors, presumably of the *Debeya-Dewalquea* complex (see also Rüffle, 1978, 1980). This is an interesting hypothesis, but there does not seem to be much evidence to support it at this time. Holly-like *Quercus* leaves have been reported from the Cretaceous and throughout the Tertiary. Ettingshausen (1896) felt that this was the primitive leaf form within the genus and that all other forms were derived. This is a common form in the section *Protobalanus,* which is held to be primitive among American oaks. Trelease (1918, 1924) believed that all the American oaks evolved from a single holly oak ancestor (i.e., a mid-Tertiary *Q. chrysolepis*-like form). A few of the early holly oak fossils may well be ancestral within *Quercus,* yet, some have been shown to belong to *Ilex* or *Nyssa* when examined more closely (Kvaček & Walther, 1981). This leaf type became common during the Miocene, when drier climates, for which this leaf type is best suited, prevailed.

Castanea-like leaves are also among the oldest to be assigned to *Quercus.* However, forms with regularly spaced, uniform teeth and secondaries do not appear until the Eocene. These "chestnut" forms may be *Quercus,* but leaves of this type are very difficult to distinguish from similar forms in other genera of Fagaceae as well as some nonfagaceous taxa. The problems of determining the generic affinities of these forms have been discussed by numerous authors (e.g., Trelease, 1924; Schwarz, 1936b; Camus, 1934–1954; MacGinitie, 1969) and have been confirmed in Jones

(1984). There are slight differences in the modern forms (particularly the nature of the multicellular "glandular" trichomes) that usually allow modern forms to be distinguished, but there are no consistent generically correlated features that can be used to assign a fossil form to an extant genus with confidence. As with all forms, cuticular information greatly enhances the chances of correctly classifying a fossil leaf type. Kräusel and Weyland (1950), for instance, used cuticular evidence to justify transfer of a fossil putative chestnut oak *Q. furcinervis* (Rossm.) Unger to the genus *Castanopsis*. Although I do not share the certainty with which Kräusel and Weyland made the transfer, the cuticle information does support their position. If the nature of the trichomes, not just the trichome bases, were known, such a transfer might be made with assurance.

Although the true affinities of many putatively fagaceous fossil leaves remain to be established, different leaf forms appear to have arisen at different times in this family. The entire and holly-like leaves from the Upper Cretaceous and Paleocene may be from the first *Quercus* species. Coarsely round-toothed and regular chestnut oak types do not appear until the Eocene. Lobed forms first occur in the Oligocene and become common in the Miocene. A thorough reexamination of fossil fagaceous leaves is needed, however, to confirm the affinities of these fossils and help resolve questions about the origin and subsequent evolution of *Quercus*.

Final Discussion and Conclusions

Leaves of the Fagaceae vary considerably within broad limits. All extant Fagaceae have simple leaves of high rank with obliquely oriented tertiary veins, anomocytic and/or cyclocytic stomatal complexes, and specific trichome complements, which depend on the intrafamilial taxon in question. Nearly all fagaceous leaves can be classified into one of the following major morphotypes: 1) entire or partially toothed, elliptical to lanceolate evergreen forms; 2) entire, broad, tardily deciduous to evergreen forms; 3) xeromorphic, sclerophyllous, small, entire-margined, evergreen forms; 4) sclerophyllous holly-like forms; 5) craspedodromous "chestnut"-like forms; 6) coarsely round-toothed, deciduous forms; 7) roundly lobed deciduous forms; 8) sharply lobed deciduous forms; and 9) narrow willow-like leaves. Many of these leaf types, however, cross taxonomic boundaries, and there is considerable foliar variability among intrafamilial taxa.

Leaves of extant Fagaceae can be distinguished from those of other families when cuticular and architectural features are available, but the intrafamilial taxonomic utility is somewhat limited because of the variability of foliar characters. Leaves of most Fagaceae can be classified at the species or species complex level. Unfortunately, leaf character differences often do not coincide with established subfamilial, generic, subgeneric, and even sectional boundaries. Thus, it is sometimes impossible to separate these intermediate level taxa without including more than one character assemblage of subordinate taxa. Some features or groups of characters are unique to specific taxa whereas other foliar syndromes can be found among several. Entire-margined evergreen leaves with type 9 trichomes, for instance, are found only in the genus *Lithocarpus* whereas regularly toothed, craspedodromous, chestnut-like leaves with types 5, 6 and 15 and/or 16 trichomes, are found in four genera and two subfamilies. Thus, classification among various intrafamilial taxa can be easy to impossible, depending on the uniqueness of the character assemblage of the leaf at hand.

Foliar information, when combined with other taxonomically useful data, contributes to our understanding of the taxonomy of this family. A classification scheme based on foliar and other data is presented in Table 2. This proposed classification scheme differs in some respects from the widely accepted scheme proposed by Forman (1966a). Leaf data, for instance, indicate that *Nothofagus* is distinct from all other Fagaceae and is, instead, closer to the Betulaceae. The doubly serrate margins and large glandular trichomes, common to *Nothofagus* and members of the Betulaceae, are rare or absent in all other modern Fagales. A distinction between *Nothofagus* and the Fagaceae sensu stricto is also apparent when pollen (Praglowski, 1982), chromosome numbers (Armstrong & Wylie, 1965), inflorescences (Reece, 1938), vegetative features such as wood (Shimaji, 1962), and phytochemical data (Oesch, 1969) are examined. Foliar information, together with that mentioned above, supports recognition of the Nothofagaceae as proposed by Kuprianova (1962) and Nixon (1982) and suggests the phylogenetic relationships illustrated in Text-Figure 5. Foliar information tells us little, however, about the intrageneric taxonomy of this genus. The entire-

TABLE 2. Proposed classification of genera traditionally considered to be fagaceous.

Nothofagaceae	Fagaceae			
	Fagoideae	Castaneoideae	Trigonobalanoideae	Quercoideae
Nothofagus	*Fagus*	*Castanea* *Chrysolepis* *Castanopsis* *Lithocarpus*	*Trigonobalanus*[a]	*Quercus*

[a] *Trigonobalanus* is a heterogeneous assemblage that should be divided when a more complete knowledge of the component species is obtained.

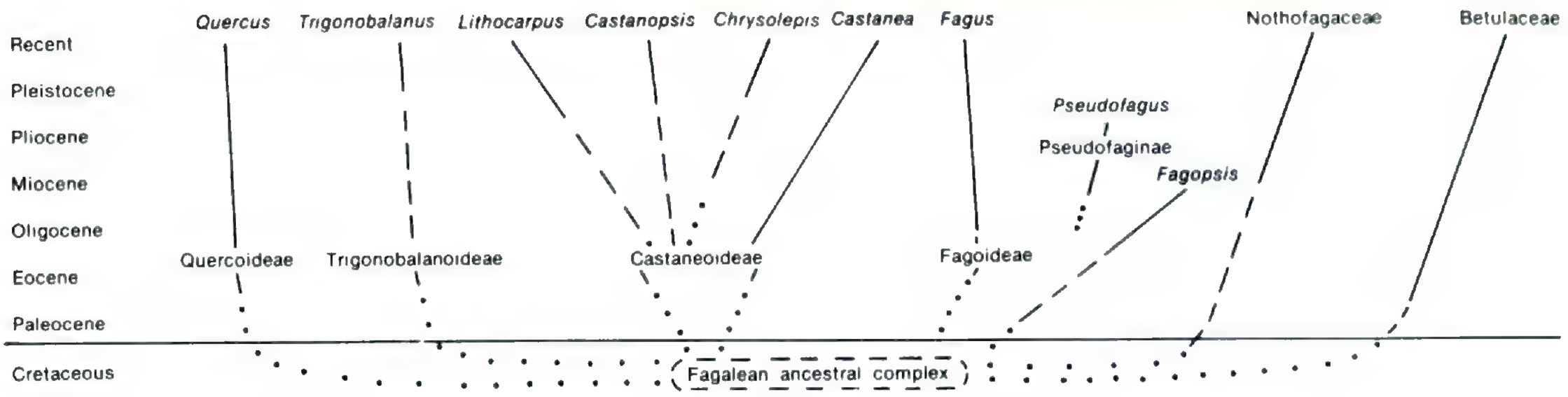
margined tropical forms (i.e., those of the 'brassi' pollen group) do seem to be a tightly knit unit, but little correlation can be found between the various lines of morphological and anatomical evidence in other groups. The lack of correlation between various lines of morphological and anatomical evidence has been noted by previous authors (Hanks & Fairbrothers, 1976). Thus, if one accepts the Nothofagaceae, recognition of the 'brassi' group as a separate genus could be justified but it would be hard to support further division of the remaining species at this level.

Fagus, often thought to be closely related to *Nothofagus,* is clearly distinguishable from this and other genera of Fagaceae and thus should be retained in its own subfamily, the Fagoideae. The uniformity of the leaves in this genus supports the lack of formal division into subgenera or sections. The leaves of the Quercoideae and Castaneoideae are most often distinguishable. However, certain forms like the "chestnut" leaf type are found in both subfamilies. This foliar overlap may be used in support of the recognition of a single subfamily, the Castaneoideae, as suggested most recently by Brett (1964). Overlap in wood anatomy, fruit, and cupule structure also obscures the distinction between these two subfamilies. Pollen morphology provides convincing evidence, however, for separating these two taxa. Another problem, at the subfamilial level, is the proposed recognition of the Trigonobalanoideae (Lozano-C. et al., 1979). The foliar characteristics of *Trigonobalanus* (e.g., tooth type, trichome complements) are sufficiently distinct from those of other Quercoideae to rationalize inclusion in a separate subfamily when considered in light of differences in chromosome numbers as well as the morphological and anatomical features reviewed by Lozano-C. et al. (1979). Removal of *Trigonobalanus* from the Quercoideae would also help sharpen the distinction between the Quercoideae and the Castaneoideae. Within *Trigonobalanus* there is sufficient foliar diversity to support further separation of this genus into discrete subgenera or even separate genera, as proposed by Erdtman (1967) on the basis of pollen form and structure.

Quercus presents numerous taxonomic problems. The division of *Quercus* into several genera, as proposed by Schwarz (1936a), is not warranted by foliar data. The intrasectional variability is great in nearly all sections and there is a great deal of overlap. The subgenus *Cyclobalanopsis* as proposed by Camus (1934–1954) is a rather discrete unit and probably merits its subgeneric status. The sections of the subgenus *Quercus* show general trends in foliar features, but the sections cannot be discretely separated using leaf characters alone.

Foliar features generally confirm the current consensus concerning generic delimitation within the Castaneoideae. *Chrysolepis* is clearly differentiable from *Castanopsis* on the basis of differences in leaf architecture and trichome complements. This supports the conclusions of Hjelmqvist (1948), Forman (1966b), and many other modern authors, who base their conclusions primarily on reproductive features. *Castanea* is a uniform and well defined taxon. The leaves share the uniformity characteristic of nearly all organs of this genus. There is little difference in the leaves, even between the two sections, *Eucastanon* and *Balanocastanon,* of this genus. Unfortunately, a few members of *Lithocarpus, Castanopsis,* and even *Quercus* possess the same general leaf architectural and cuticular features making identification to the generic level difficult.

In *Castanopsis* there are few differences among the leaves of most sections, and thus foliar features cannot be used to support these sectional divisions. Foliar data do support retention of the *Castanopsis fissa* group within *Castanopsis* rather than placement in *Lithocarpus.* This is in ac-



TEXT-FIGURE 5. Possible phylogenetic relationships within the Fagales.

cordance with the findings of Luong (1965) and Forman (1966b) based on infructescence studies.

It is apparent that *Lithocarpus* is a large and relatively unstudied genus that requires further taxonomic revision. The leaves of this group, as currently circumscribed, are fairly uniform in gross morphology but trichome differences, particularly the absence of type 9 trichomes in relatively few specimens, provide incentive for the much needed revision of this group. It does appear that *Lithocarpus densiflorus* stands apart from all other members of this genus and there is some indication that *Limlia* may deserve recognition as a separate genus. Additional conclusions concerning the impact of foliar data on the classification of other infrageneric taxa in this and some other genera of Fagaceae must await analysis of a more complete sample.

The potential for identifying and correctly classifying fossil fagaceous leaves diminishes as the age of the material increases. Although this is substantially intuitive, the age at which one must use extreme caution when assigning materials to modern genera or subfamilies is much more recent than one might have expected only a decade ago. The recent discovery of *Pseudofagus* (Smiley & Huggins, 1981) and the reinterpretation of *Fagopsis* (Manchester & Crane, 1983) serve to illustrate that leaves similar to those of extant genera can be found on plants of extinct genera and subfamilies, in sediments as young as the Miocene. The strength of any determination based on leaves must therefore rest substantially on correlation with fossils of other more definitive organs. The ability to determine the affinities of more recent materials will depend, as with modern leaves of this family, on how unique the particular leaf type is within the family.

The time and place of origin of the Fagaceae is still largely a mystery. No leaves or other organs definitely assignable to the Fagaceae have been found prior to the Eocene. The diversity present in the Eocene, however, suggests an origin at least as early as the Paleocene. The existence of primitive Fagaceae, or possible precursors thereof, in the Cretaceous (Santonian) of North America is indicated by the recent discovery of a "fagalean" flower by Friis (pers. comm.) and Tiffney (pers. comm.). The ability to identify early remains as Fagaceae may well be limited by the existence of vegetative and reproductive strategies, such as wind and/or water fruit dispersal, alien to modern Fagaceae with which we are familiar. The modern large animal dispersed fruits, that is, acorns, chestnuts, and beechnuts, do not appear until the Eocene (Tiffney, 1984). Their development was probably a function of coevolution with small mammals, for example, rodents. Rodents first appear in the uppermost Paleocene and squirrels, which commonly disperse modern fagaceous fruits, evolved in the late Eocene (Romer, 1966). It is reasonable to assume then that Paleocene and earlier forms would have gross fruit morphologies unlike those of modern members of the family. Similar trends in fruit evolution occur in the Juglandaceae (Manchester, 1981b) and most likely the Betulaceae as well.

Most modern authors contend that the Fagaceae arose in the Northern Hemisphere late in the Cretaceous. The presence of *Nothofagus* in the Southern Hemisphere does not contradict this conclusion if one considers the relation of this taxon to the Fagaceae sensu stricto and the Betulaceae. If *Nothofagus* is closer to the Betulaceae and merits distinction as a separate family, it more than likely evolved independently from a common fagalean ancestor during the late Cretaceous. This ancestor or ancestral complex probably extended its range southward, or northward according to Schuster (1972), at or prior to this time. This migration may well have occurred through Africa, as Raven and Axelrod (1974)

have suggested. Examination of the Upper Cretaceous floras of Africa for evidence of fagalean fossils is needed to help test this hypothesis.

The known fossil record suggests that the Nothofagaceae evolved from this primitive fagalean complex in the Southern Hemisphere (probably in southern Australia or Antarctica) while the Fagaceae sensu stricto evolved from representatives of the same complex in the Northern Hemisphere. The fossil record indicates, with minor recent exceptions, that neither family has occurred in any hemisphere other than that in which it is found today. It is extremely difficult to be more specific about the place in which the Fagaceae sensu stricto evolved. It has been noted that American forms of both *Fagus* and *Quercus* have been found previously in Europe and that European forms have not been found in North America. It also seems that the greatest diversity has existed on the Eurasian land mass. Whether diversity is a good indicator of the site of origin of a taxon remains to be proven. The fossil record, upon which final resolution of this problem must depend, is not known well enough to confirm southeast Asia, as many have suggested, or any other hypothesized locus, as the site of origin for the Fagaceae.

We know little more about the nature of the first Fagaceae. When the first firm record of the Fagaceae appears (in the Eocene) we have both the Castaneoideae and Quercoideae represented in fairly modern form. The first records of modern genera are *Castanea* and *Quercus,* but neobotanists have generally considered these to be derived forms within the family. *Lithocarpus, Castanopsis, Chrysolepis,* and *Trigonobalanus* are the genera that are usually cited as candidates for evolutionary 'Urpflanzen' within this group. Given the different selective pressures, particularly those associated with fruit dispersal, it seems likely that the earliest Fagaceae would be different from all modern genera. *Fagopsis* fits the idealistic image of a primitive fagaceous form but reproductive material has been confirmed only in the Eocene and early Oligocene, too late to indicate ancestral affinities. If, however, Paleocene leaves assigned to *Q. groenlandica* can be shown to be *Fagopsis,* as Wolfe (1977) suggested, this genus would likely be part of the ancestral fagaceous complex.

When the mutual characteristics of the Betulaceae, *Nothofagus,* and the Fagaceae sensu stricto are considered, we might expect the ancestral plexus to consist of wind dispersed "amentiferous" forms with irregularly toothed (perhaps doubly serrate), craspedodromous, simple leaves. Such leaves have been found in the late Cretaceous and have been attributed to the Betulaceae (Wolfe, 1973). Crane (1981), however, indicated that the first solid evidence of the existence of the Betulaceae occurs in the Paleocene. Whether or not these leaves are betulaceous, fagaceous, *Nothofagus,* or some fagalean intermediate can be determined only when reproductive materials are found and analyzed.

There does seem to be a pattern to the appearance of various leaf forms in the Fagaceae. If we disregard the Cretaceous leaf forms as suggested by Wolfe (1973), the first fagaceous leaves appear to be irregularly serrate, simple, pinnate forms with percurrent tertiaries obliquely disposed in relation to the midrib. Many of these occur in the Paleocene and have been placed in the genus *Dryophyllum* by previous workers. During the Eocene we have the appearance of the "chestnut" leaf type and coarsely round-toothed oak leaves. The first sharply lobed oaks appear in the Oligocene and become abundant in the Miocene. The earliest record of round-lobed leaves occurs in the Miocene where they are particularly abundant in Eurasia. Because of numerous homeomorphies, it is difficult to know which of the fossil holly-like forms and laurel forms are truly fagaceous. In spite of their alleged antiquity, fagaceous holly-like forms may not have arisen until the climatic deterioration at the end of the Eocene and did not become abundant until the Miocene. It is also impossible to know which of the laurel-like and other entire-margined forms are fagaceous until the nature of their cuticles has been determined.

Rüffle and co-workers (see Rüffle, 1980) have proposed the only phylogenetic model for this group based on leaves. They maintained, largely on the basis of cuticular resemblance, that the Fagaceae or fagalean ancestors extend back into the Cretaceous where they blend with the palmately lobed and palmately compound *Debeya-Dewalquea* complex. According to this hypothesis, these types form a bridge between the palmate platanoid complex and the pinnate fagaceous types with which we are familiar. Rüffle and Knappe (1977) also contended that the lobed oaks, for example, *Q. falcata,* are atavistic expressions of the early platanoid types. This is a very intriguing hypothesis, which may be correct, yet the cuticular evidence that these workers cite is not very strong. No trichome data are

offered and the characters that are consistent with those of the Fagaceae (e.g., anomocytic stomatal complexes) are common to many other taxa as well. The validity of this proposal must be tested by rigorous examination of relevant fossil leaf forms in conjunction with the pioneering work on reproductive materials being conducted by Crepet, Daghlian, Manchester, and others.

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APPENDIX I

A FOLIAR "KEY" FOR CONFIRMING FAGACEOUS AFFINITIES AMONG MEMBERS OF THE HAMAMELIDOPSIDAE (AMENTIFERAE)

The following "key" is designed to help confirm the identity of fagaceous leaves among similar forms in the Hamamelidopsidae sensu Cronquist (1981). It is based on broad summary publications (e.g., Lawrence, 1951; Metcalf & Chalk, 1950, 1979; Hutchinson, 1967; Willis, 1973; Cronquist, 1981), familial surveys (e.g., Winkler, 1904; Sheffy, 1972), personal communications with those working with amentiferous leaves, and personal observations.

1. Stomata anomocytic or cyclocytic 2
1. Stomata neither anomocytic nor cyclocytic ..... Balanopaceae
Barbeyaceae
Casuarinaceae
Cercropiaceae
Daphniphyllaceae
Hamamelidaceae
Moraceae pro parte
Platanaceae pro parte
Tetracentraceae
Trochodendraceae
Ulmaceae pro parte
Urticaceae pro parte

2. Leaves simple 3
2. Leaves compound ..... Cannabidaceae pro parte
Juglandaceae
Moraceae pro parte
Rhoipteliaceae

3. Leaves with pinnate venation 4
3. Leaves with distinctly acrodromous or flabellate venation ..... Cannabidaceae pro parte
Cercidophyllaceae
Moraceae pro parte
Myrothamnaceae
Platanaceae pro parte

4. Leaves, when toothed, possessing craspedodromous secondary veins 5
4. Leaves toothed without purely craspedodromous secondary veins ..... Eucommiaceae
Platanaceae pro parte

5. Leaves lacking anastomosing, fibrous, fine venation and strong marginal veins; areolation well developed consisting of small orthogonal, nearly isodiametric units 6
5. Leaves possessing anastomosing, fibrous, fine venation; strong marginal veins and elongate areoles ..... Didymelaceae

6. Leaves, when toothed, possessing less than two teeth per secondary over more than half of the leaf length; or as in some *Nothofagus* species, with more than two teeth per secondary over more than two-thirds of the leaf length and always possessing simple unicellular (type 1) trichomes and often large glands (type 17) 7
6. Leaves serrate with more than two irregularly spaced teeth per secondary; trichomes restricted to uniseriate nonglandular forms ..... Eupteliaceae

7. Leaves usually bearing symmetrical bases; epidermal idioblasts absent; types 1 and 2 trichomes, when present, lack hooks; type 3 trichomes, when present, possess unicellular bases; epidermis neither calcified nor silicified 8

7. Leaves frequently with markedly asymmetrical bases; idioblasts (e.g., Lithocysts) common in the upper epidermis; short unicellular trichomes (types 1 and 2) common and often hooked; type 3 trichomes when present are borne on multicellular bases; epidermis frequently calcified or silicified ..... Cannabidaceae pro parte, Moraceae pro parte, Ulmaceae pro parte, Urticaceae pro parte
8. Thick-walled type 1 trichomes, when present unicellular 9
8. Trichomes resembling type 1 always multicellular with thin cross septae ..... Leitneriaceae
9. Leaves neither linear-oblong and pinnatifid with semicordate stipules, nor spatulate with prominent looping secondaries; glandular scales, when present, subtended by simple trichome bases 10
9. Leaves with glandular scales subtended by bicellular (rarely tri- or tetracellular) bases, or when absent, leaves linear-oblong and pinnatifid with semicordate stipules, or leaves spatulate with prominant looping secondaries ..... Myricaceae
10. Leaves rarely doubly serrate; when doubly serrate, serrate over more than two-thirds of the lamina length possessing only types 1, 2 and often type 17 trichomes ..... Fagaceae
10. Leaves nearly always doubly serrate possessing modified and/or uniseriate multicellular trichomes and/or glandular trichomes in addition to types 1 and 2 ..... Betulaceae

Appendix II

Key to the genera of Fagaceae (based on foliar features)

1. Leaves lobed 2
1. Leaves not lobed 4
2. Upper cuticles revealing sinuate anticlinal walls; may possess only trichome types 1 and 15, never tufts ..... *Fagus* (some cultivars)
2. Upper cuticles revealing straight to slightly curved anticlinal walls; may possess a variety of trichome types including tufts of various sorts 3
3. Lobes nearly always pointed and aristate ..... *Quercus* (sect. *Erythrobalanus* pro parte)
3. Lobes rounded and nonaristate ..... *Quercus* [sects. *Erythrobalanus* (rare), *Lepidobalanus, Mesobalanus,* and *Cerris* pro parte]
4. Leaves bearing persistent yellowish, peltate (type 11) trichomes ..... *Chrysolepis*
4. Leaves not bearing persistent yellowish, peltate (type 11) trichomes 5
5. Leaves usually bearing large globular (type 17) trichomes, or curly thin-walled (type 12) trichomes forming a dense cover over the lower surface of the leaf and/or type 2 trichomes common over major veins; all leaves lacking tufts; teeth, when present, compound or biconvex (type A1) ..... *Nothofagus*
5. Leaves never bearing type 17 trichomes; teeth nearly always simple; type 2 trichomes not abundant and when present usually restricted to the midrib or petiole; type 12 trichomes rare and never forming a dense mat 6
6. Upper cuticles of mature leaves revealing sinuous anticlinal walls; secondary veins strictly craspedodromous and very straight except near the base of the leaf where they often recurve; trichomes restricted to types 1, 15 and rarely 2 ..... *Fagus* pro parte (all except lobed cultivars)
6. Upper cuticles of mature leaves generally lacking sinuous anticlinal walls; secondary veins craspedodromous or camptodromous usually slightly curved, or less regular and straight; trichomes usually include tufts in addition to or instead of trichome types 1 and 15 7
7. Lower cuticles bearing appressed parallel (type 9) trichomes *Lithocarpus* pro parte
7. Lower cuticles without type 9 trichomes 8
8. Leaves strictly craspedodromous, lacking intersecondary veins; secondary veins regular and straight to slightly curved; teeth regularly spaced 9
8. Leaves camptodromous or craspedodromous with irregularly spaced secondaries; intersecondaries often present 14
9. Teeth not rounded and often spinose 10
9. Teeth rounded and fairly coarse ..... *Quercus* (sects. *Lepidobalanus, Mesobalanus,* and *Cerris* pro parte
10. Leaves lacking large multiradiate (type 10) trichomes 11
10. Leaves bearing large type 10 trichomes ..... *Lithocarpus* (*L. densiflorus* only)

11. Leaves with abundant thin-walled peltate (type 13) trichomes, with darkly staining bases, on the lower surface ..... *Castanopsis* pro parte
11. Leaves lacking type 13 trichomes 12
    12. Leaves lanceolate, subcoriaceous, nearly glabrous at maturity with only simple trichome bases widely scattered on the epidermis; upper cuticles with sinuate anticlinal walls 13
    12. Leaves chartaceous (rarely subcoriaceous) bearing at least the proximal portions of simple uniseriate (type 15) and/or capitate (type 16) trichomes; tufts (types 5 and 6) usually present and often abundant; upper cuticle revealing straight to rounded anticlinal walls ..... *Quercus* (sects. *Cerris, Cyclobalanopsis, Erythrobalanus, Lepidobalanus,* and *Macrobalanus* pro parte *Castanea*
        13. Leaves with greater than 11 pairs of secondary veins ..... *Lithocarpus* pro parte (*L. cornea*)
        13. Leaves with fewer than 11 pairs of secondary veins ..... *Quercus* (sect. *Cyclobalanopsis* pro parte)
            14. Leaves holly-like, coriaceous to sclerophyllous secondaries usually irregularly spaced, often entering large spinose teeth ..... *Quercus* (sects. *Erythrobalanus* pro parte, *Lepidobalanus* pro parte, and *Protobalanus*)
            14. Leaves entire or partially toothed, not holly-like 15
                15. Leaves entire or toothed only near the apex; apex caudate or attenuate (rarely, simply acute), often forming a drip tip 16
                15. Leaves entire or with irregularly spaced bristle bearing teeth; apex not caudate and not bearing a drip tip 17
                    16. Lower cuticle speckled with darkly staining thin-walled peltate (type 13) trichome bases; type 13 trichomes often present in abundance ..... *Castanopsis* pro parte
                    16. Lower cuticle lacking type 13 trichomes; darkly staining bases, when present, subtending one or more of trichome types 15, 16, and 17 ..... *Quercus* (sect. *Cyclobalanopsis* pro parte) *Lithocarpus* pro parte
                        17. Leaves entire-margined, sclerophyllous; with large multiradiate (type 10) trichomes ..... *Lithocarpus* (entire-margined *L. densiflorus*)
                        17. Leaves not bearing type 10 trichomes 18
                            18. Leaves possessing "glandular" peltate (type 19) trichomes or thin uniseriate (type 15) trichomes with very broad, darkly staining, basal cells (Jones, 1984, pl. 52D) or secondary veins that end nearly in the sinus above the teeth, as in Jones (1984, pl. 14A, B, D) ..... *Trigonobalanus*
                            18. Leaves without any of the above characteristics ..... *Quercus* (sects. *Erythrobalanus, Lepidobalanus,* and *Macrobalanus* pro parte)

APPENDIX III

CLASSIFICATION OF TRICHOMES OF THE FAGACEAE

Trichomes have been used taxonomically in parts of the Fagaceae for many years (Dyal, 1936; Hardin, 1975, 1979; Thomson & Mohlenbrock, 1979), yet no one has adequately surveyed the trichomes in the entire family. Camus (1934–1954) provided a truly remarkable analysis but she did not investigate the Fagoideae and her data from the Castaneoideae and Quercoideae is lost in a sea of other morphological and anatomical data. Like most neobotanists, she tailored her work for use on modern plants and neglected some of the less taxonomically useful features upon which paleobotanists must often rely. Her study is undoubtedly the most complete, but she failed to thoroughly classify and interpret the trichomes she observed. Hardin (1976) provided a good analysis in his series of papers on the trichomes of *Quercus* species from the southeastern United States, however, the taxonomic scope of this work is fairly limited. The following is an attempt to classify and describe the major trichome types found among all extant Fagaceae. This classification is built historically on those of Camus, Dyal, Hardin, and others. The classification must be arbitrary in many respects because most forms intergrade with at least one other type and discrete boundaries usually do not exist. I have attempted to combine forms that cannot be distinguished without sectioning or other time consuming methods. All types listed here can be identified through examination of whole leaf material with a standard light microscope or a scanning electron microscope. I have divided the trichome types into three major groups; nonglandular, intermediate, and glandular. As in the classification schemes of earlier authors, the terms glandular and nonglandular are not strictly correlated with the functions they imply. They are, rather, terms that roughly describe the apparent function of the trichome types. Each term is associated with a syndrome or combination of characteristics under the lettered headings below.

A. "Nonglandular" trichomes. Trichomes of this group are generally thick-walled, apparently nonglan-

dular, and unicellular or composed of unicellular elements. The function of these trichomes appears to be related to physical protection or "covering." This class corresponds fairly well to the "poils tecteurs" of Camus (1928–1929, 1934–1954).

Type 1 (solitary unicellular). Trichomes of this type are usually thick-walled, fairly long, and straight to slightly wavy in course (Fig. 1). In those species in which they occur on fine veins, they are usually erect, bristle-like, and relatively short (Fig. 2). When restricted to the petiole, midrib, and other major veins, these trichomes tend to be longer and somewhat appressed to the vein from which they arise. These long appressed forms are usually thinner walled and frequently occur in young leaves. They are not as resistant as the short erect ones and tend to be lost with time. This rather fragile form conforms to "poils tecteurs unicellules courbés a la base" of Camus (1934–1954, volume III). Trichome type 1 is perhaps the most widely dispersed trichome type in the Fagaceae and is found in all genera (see Table 2). This trichome type appears to form one end of a continuum from solitary unicellular trichomes to the many element type 6 tufts. Type 1 trichomes are most abundant and reach their highest development in *Fagus* and some *Nothofagus,* in which they cover the major veins and margins of young leaves (Fig. 3). Many of these trichomes are lost as the leaf ages, but a few usually can be found in protected areas on or near the midrib. This trichome type corresponds to "poils tecteurs (unicellulaires) isolés" of Camus (1928–1929, 1934–1954) and "solitary" of Hardin (1976).

Type 2 (unicellular conical). Trichomes of this type are short, thick-walled, and erect (Fig. 4). They are generally restricted to the major veins as well. Some, particularly in *Nothofagus,* have a distinctive, darkly staining, broad basal portion (thickened foot cell of Hill, 1983a) (Fig. 5). There is essentially no difference between types 1 and 2 trichomes other than length. Yet, the taxonomic distribution of these short trichomes and their resultant systematic utility justify their separation into a distinct type. This trichome type is best developed in the genus *Nothofagus* and is rare outside the Fagoideae sensu lato.

Type 3 (papillae). Papillae are included here, though straining application of the term trichome, because they intergrade with broad-based type 2 trichomes. They are relatively rare in the Fagaceae, occurring only in a few species of *Quercus* and *Lithocarpus* and one species of *Nothofagus.* When present they adorn nearly all otherwise undifferentiated lower epidermal cells (Figs. 6, 7) except in *N. obliqua,* in which they are restricted to the adjacent epidermal cells of stomatal complexes. They are thick-walled and arise from normal-sized epidermal cells.

Type 4 (appressed laterally attached unicellular). These trichomes resemble type 1 except that they are attached laterally and are generally thin-walled. It is often difficult to determine the point of attachment using standard methods of examination. Camus (1934–1954) illustrated a number of these from young leaves (Fig. 8). They are exceedingly rare on mature leaves, where they are confined to the larger veins. Their presence appears to be restricted to the genus *Quercus.* These correspond to the "poils unicellulaires apprimes, en navette" of Camus (1934–1954) and "appressed laterals" of Hardin (1976).

Type 5 (fasciculate). These "nonglandular" trichomes are characterized by the possession of two or more (generally four to seven) unicellular, thick-walled elements joined together only at the base. The elements may be erect and travel parallel to each other, forming a closed tuft (Fig. 9), or they may splay out to varying degrees (Fig. 10) eventually to intergrade with stellate forms. Those with very long elements often intertwine (Fig. 11). Fasciculate tufts occur in a sessile form that is usually associated with radially septate bases, and a pedicellate form, in which there is a very short epidermal pedestal upon which the rays are borne. Fasciculate tufts are found in greater abundance near major veins in most mature leaves but may form a dense cover, in some species, obscuring the entire lower leaf surface. Like most, trichomes of this type are much more common and longer on the lower leaf surface. This trichome type is restricted to the Castaneoideae and Quercoideae. It reaches its greatest development in the genus *Quercus.* This type corresponds to some of Camus' (1928–1929, 1934–1954) "poils fascicules en bouqets ou buissons, a articulés libres." However, Camus included types 8, 10, and 14 in this broad group as well. Hardin's (1976) "fasciculate" included those assigned to this group plus those of type 8, which he considered to be a subtype.

Type 6 (stellate). Stellate trichomes consist of three or more "nonglandular," unicellular, and generally thick-walled elements that radiate from a common point of attachment in a fashion parallel, or nearly parallel, to the leaf surface (Fig. 12). These trichomes are usually smaller than erect tufts, which may occur on the same leaf. They frequently can be distinguished from "open" forms of type 5 trichomes by the prominent pie-shaped wedges produced at the juncture of the constituent elements (Figs. 13, 14). Two forms of this trichome have been observed. Elements of the more common form occupy a common plane. The second form is bilayered and contains a second set of elements in a plane above the first (Fig. 15). Stellate trichomes, when abundant, are scattered evenly over the fine venation of the lower surface. They rarely occur on the upper surface. They are usually restricted to large veins or sometimes only the petiole, particularly in specimens where they are rare. They are present in both the Castaneoideae and Quercoideae and reach their greatest development in *Quercus* and *Castanea.* These conform directly to Hardin's (1976) "stellate" type except that it includes bilayered forms that according to his classification would be multiradiate. Camus (1934–1954) used the term "poils étioles" for these although some of those she classified as "poils fascicule's" are included here.

Type 7 (fused stellate). Fused stellate trichomes resemble the above except that the rays are fused for a significant portion of their length. They are fused beyond the tapered portion of the basal union (Figs. 16, 17). They generally possess a larger number of elements than type 6 (sometimes as many as 18). These are common only in *Quercus* and reach their greatest development in subsection *Virentes* of the white oak group. They are most commonly found distributed over the lower surface of the leaf. Plants that bear fused stellate trichomes usually inhabit warm coastal environments where windy conditions and sandy soil prevail. This

is equivalent to Hardin's (1976) type of the same name. Camus did not distinguish trichomes of this type from other stellate forms.

Type 8 (stipitate fasciculate). Stipitate fasciculate trichomes are similar to type 5 except that the cells are fused well beyond the base (Fig. 18). They intergrade with type 5, but differences in their taxonomic and physical distributions warrant recognition as a separate type. They are usually found in the angles of the secondary veins on the lower sides of the leaves. However, they are scattered over the fine veins as well in a few specimens (Fig. 19). In some cases the elements are extremely long and intertwine (Fig. 20). They are found only in *Quercus* and, rarely, *Lithocarpus*. They reach their maximum development in *Quercus* section *Erythrobalanus*. Sessile forms have been observed but most are pedicellate (Fig. 21). Hardin (1976) considered this a subtype of "fasciculate" trichomes.

Type 9 (appressed parallel tuft). This "nonglandular" trichome type consists of two or more generally thick-walled, unicellular elements that are nearly coplanar and approximately parallel with the leaf surface and each other (Fig. 22). The bases of the elements form a linear band rather than a rounded mass (Fig. 23). They are restricted, with few exceptions, to *Lithocarpus*, where they occur in nearly all specimens. They are one of the salient characteristics of *Lithocarpus* leaves. Camus (1934–1954) classified these trichomes under the category "poils en doigts de gant" or hairs like fingers of a glove.

Type 10 (multiradiate). These "nonglandular" trichomes are composed of several (ca. eight), unicellular, generally thick-walled, elements that emerge in a variety of seemingly random directions from a typically rounded common base (Fig. 24). These are usually found distributed over the lower surface of the lamina. This type is generally restricted to the genus *Quercus* but a particularly large and impressive form is found on leaves of *L. densiflorus* (Figs. 25, 26). This is the only occurrence, outside of *Quercus*, noted in this study. Camus (1934–1954) included the *L. densiflorus* form in her "poils étioles." Hardin (1976) included these in a group of the same name.

B. Intermediate trichomes. Trichomes assigned to this group consistently show a combination of the characteristics of "glandular" and "nonglandular" forms.

Type 11 ("thick"-walled peltate). These trichomes consist of a uniseriate stalk, which bears a somewhat circular cap of radially fused, relatively thick-walled cells. These trichomes are most often yellowish and cover the entire lower epidermis (Figs. 27–29). Although many are lost with age, they are abundant even in mature leaves. These scales are unique to, and characteristic of, the genus *Chrysolepis*. They are similar to type 13 trichomes (Fig. 33) but differ in a number of ways: they are smaller (average radius ca. 100 μm versus 180 μm), have thicker cell walls, contain yellowish resinous material, and perhaps most importantly, the cellular components of the cap tend to be radially fused (Fig. 27), which is not the case in those of type 13 (Fig. 33). Camus (1928–1929) included this in her "poils écailleux."

Type 12 (curly thin-walled unicellular). Trichomes of this type are thin-walled and collapse upon drying even in mature leaves. There is no evidence of glandular function. These persistent trichomes are coiled and unicellular. They occur in abundance only on type IV *Nothofagus* leaves, where they form dense mats over the lower surface (Figs. 30–32).

Type 13 ("thin"-walled peltate). This trichome type

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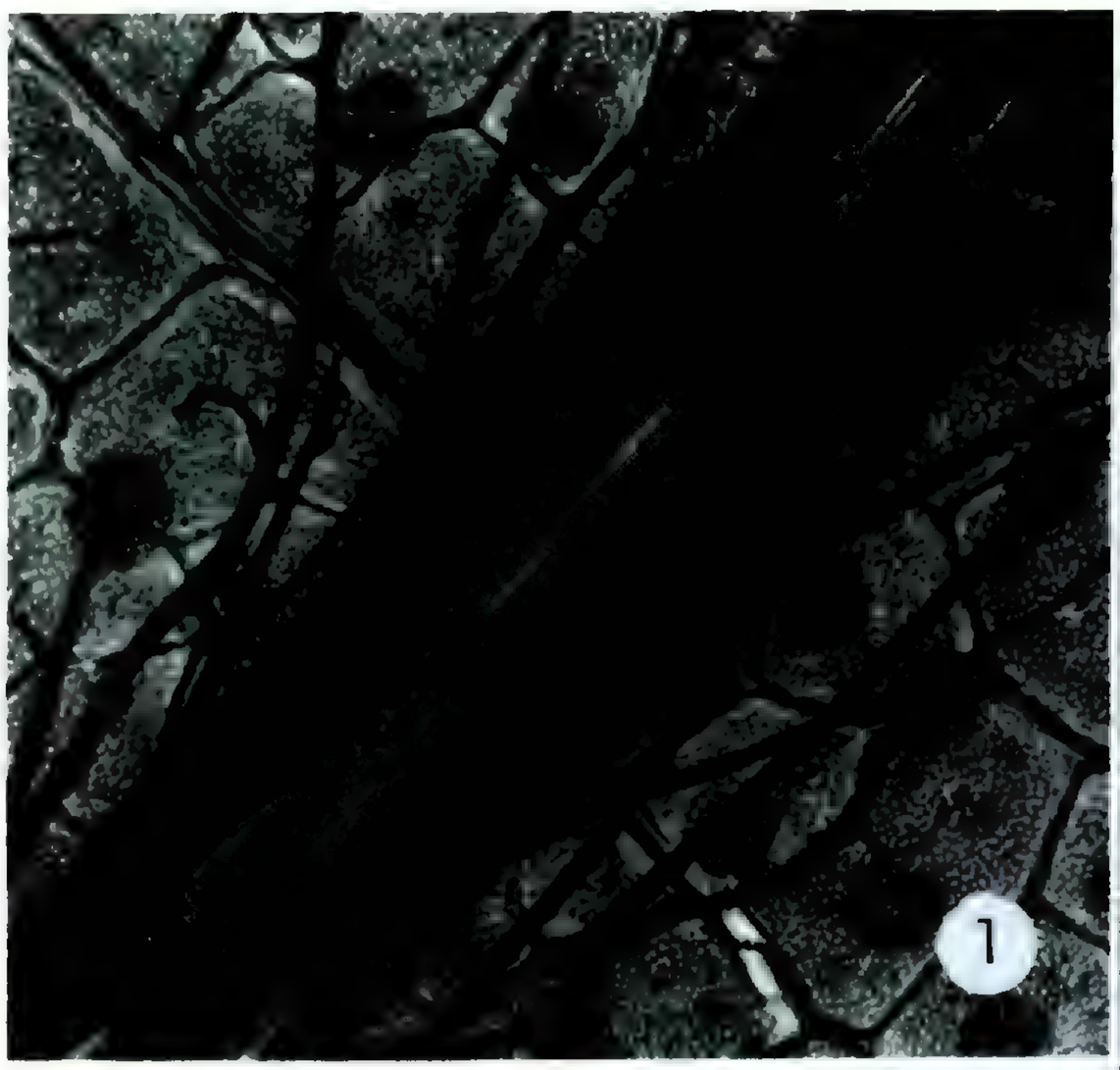
FIGURES 1–6.—1. Photomicrograph of solitary unicellular (type 1) trichomes over a secondary vein in *Nothofagus alessandri* (3115); note also the large globular (type 17) trichomes over the fine venation, 250×.—2. Scanning electron micrograph of short erect type 1 trichomes over fine venation, *Castanea mollissima* (110), 125×.—3. Photomicrograph of type 1 trichomes on the margin of *Nothofagus alessandri* (3115), 100×.—4. Scanning electron micrograph of unicellular conical (type 2) trichomes on *Nothofagus pumilio* leaves (3131), 500×.—5. Photomicrograph of type 2 trichomes showing broad basal portions, upper cuticle of *Nothofagus antarctica* (3117), 250×.—6. Photomicrograph of papillae (type 3 "trichomes") on the lower epidermis of *Quercus myrsinaefolia* (1183), 640×. [Note: Numbers in parentheses are Indiana University Paleobotanical Extant Leaf Collection accession numbers. See Jones (1984) for herbarium and collector information.]

FIGURES 7–12.—7. Scanning electron micrograph of papillae on the lower surface of *Quercus myrsinaefolia* (1183), 500×.—8. Appressed laterally attached unicellular (type 4) trichomes (redrawn from Camus, 1934), ca. 200×.—9. Scanning electron micrograph of a "closed" fasciculate (type 5) trichome from the lower surface of *Lithocarpus sundaicus* (3110), 250×.—10. Scanning electron micrograph of an "open" fasciculate trichome from the lower surface of *Quercus alba* (137), 125×.—11. Scanning electron micrograph of a type 5 trichome with long intertwining elements, *Quercus benthami* (631), lower surface, 125×.—12. Scanning electron micrograph of a stellate (type 6) trichome from *Castanea mollissima* (110), lower surface, 250×.

FIGURES 13–18.—13. Scanning electron micrograph of sprawling type 6 trichomes interspersed among type 16 trichomes, upper leaf surface of *Castanea mollissima* (110), 250×.—14. Photomicrograph of type 6 trichomes showing prominent pie-shaped wedges at the juncture of the elements, lower cuticle of *Castanea ozarkensis* (111), 250×.—15. Scanning electron micrograph of a bilayered stellate (type 6) trichome on the lower leaf surface of *Quercus arkansana* (610), 250×.—16. Scanning electron micrograph of a fused stellate (type 7) trichome on the lower foliar surface of *Quercus fusiformis* (3144), 500×.—17. Photomicrograph of type 7 trichomes on the lower leaf surface of *Quercus fusiformis* (3144), 250×.—18. Scanning electron micrograph of stipitate fasciculate (type 8) trichomes on the lower leaf surface of *Quercus crassipes* (640), 250×.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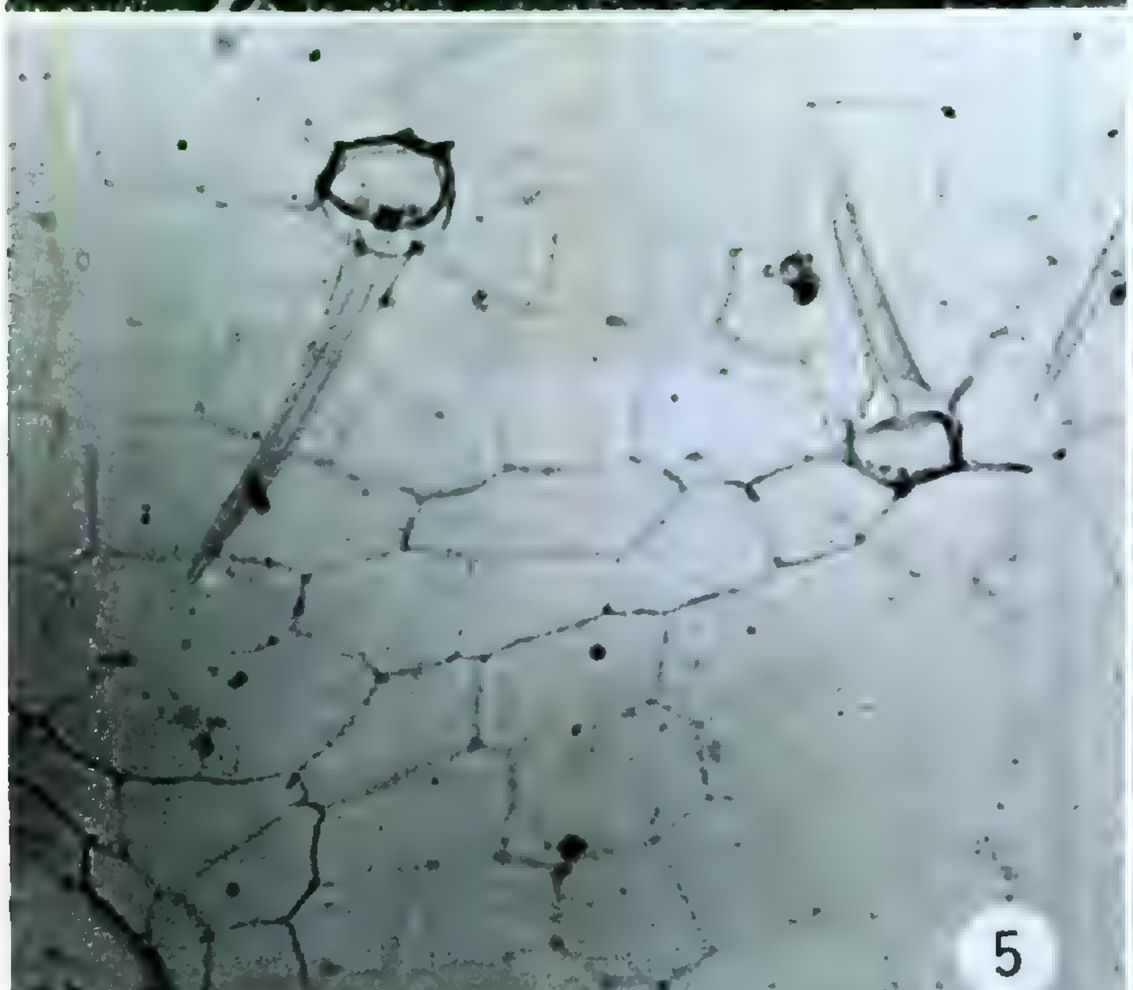
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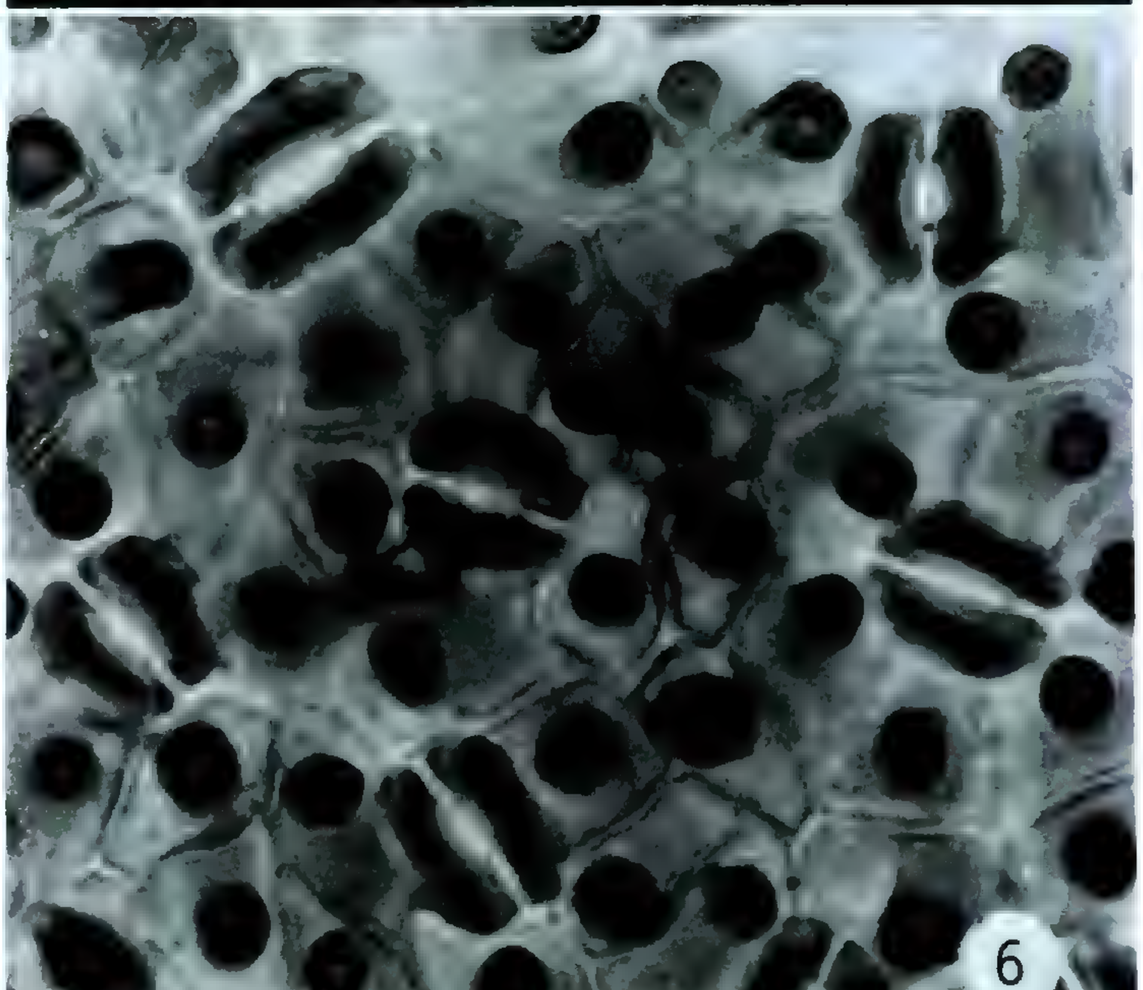
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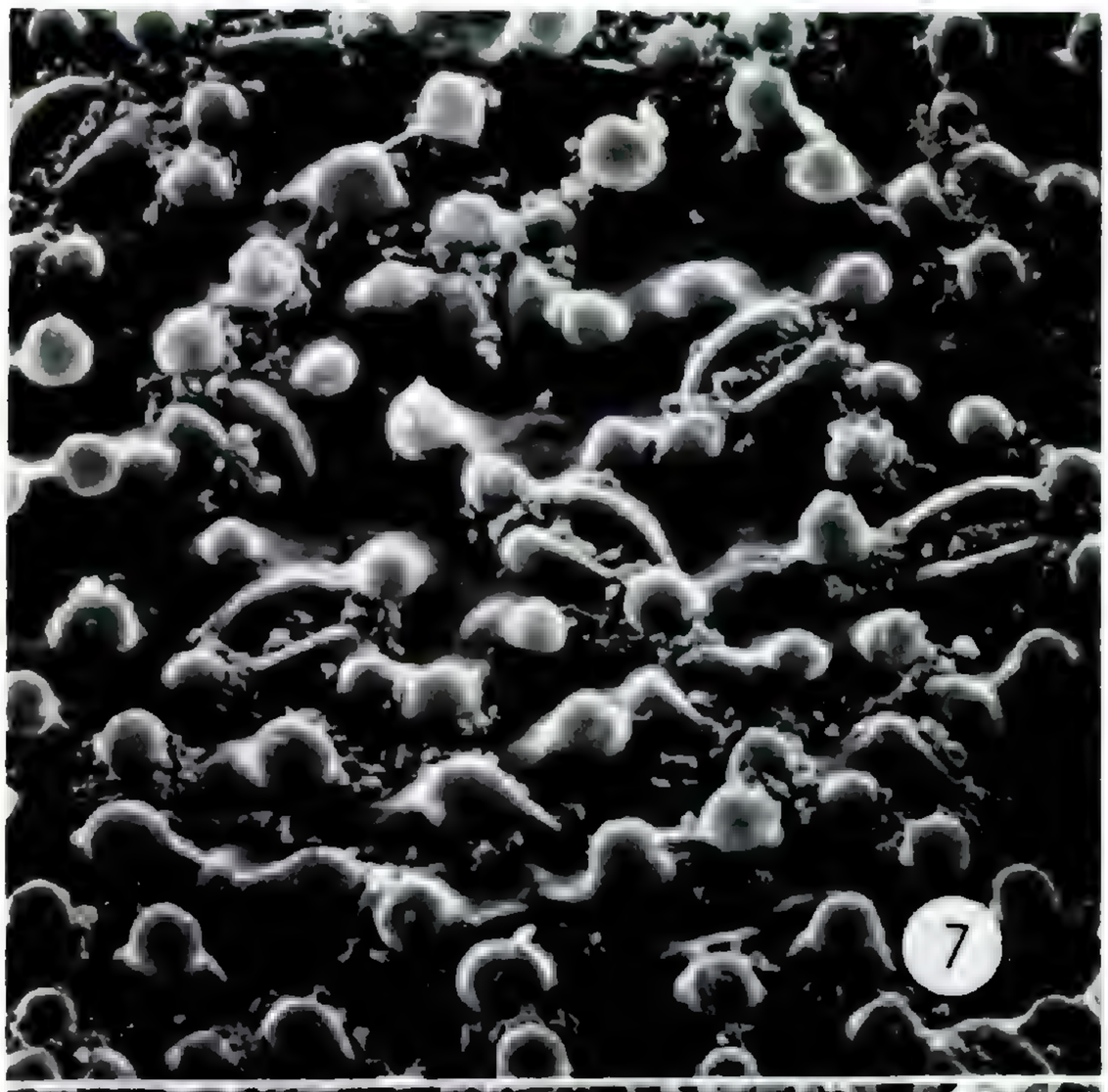
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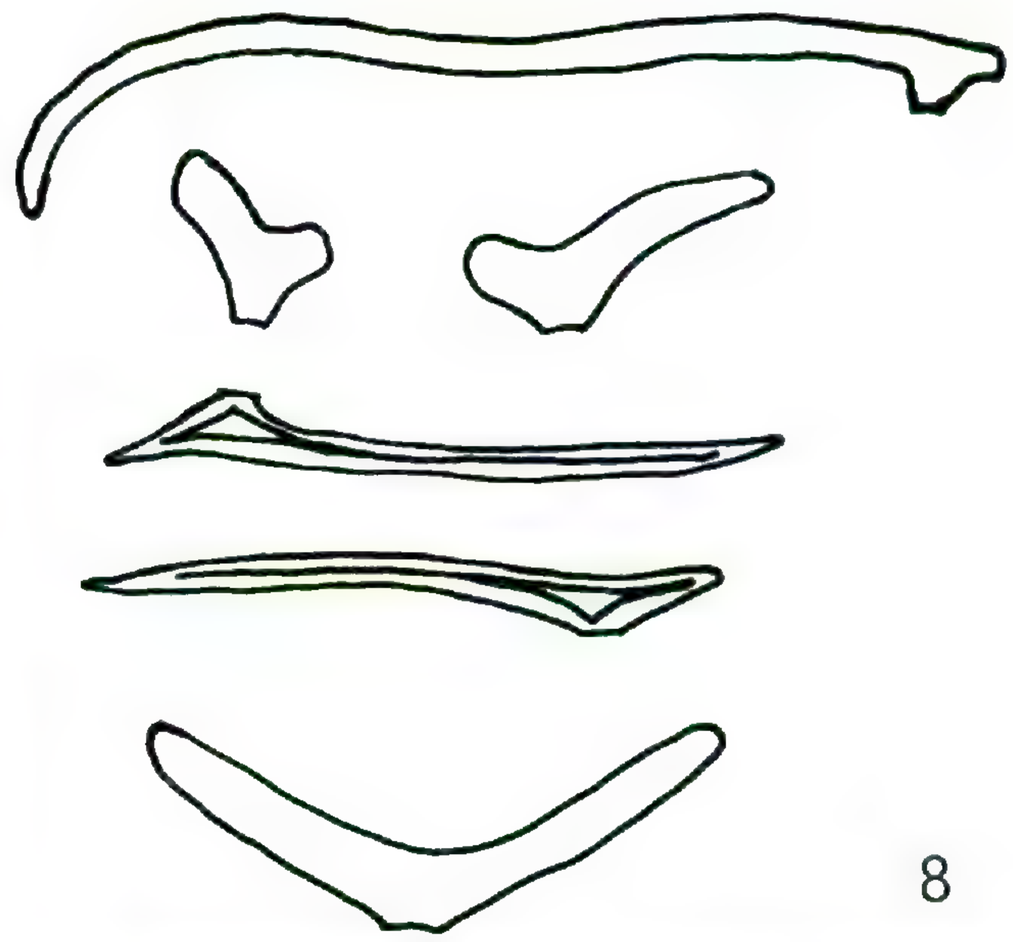
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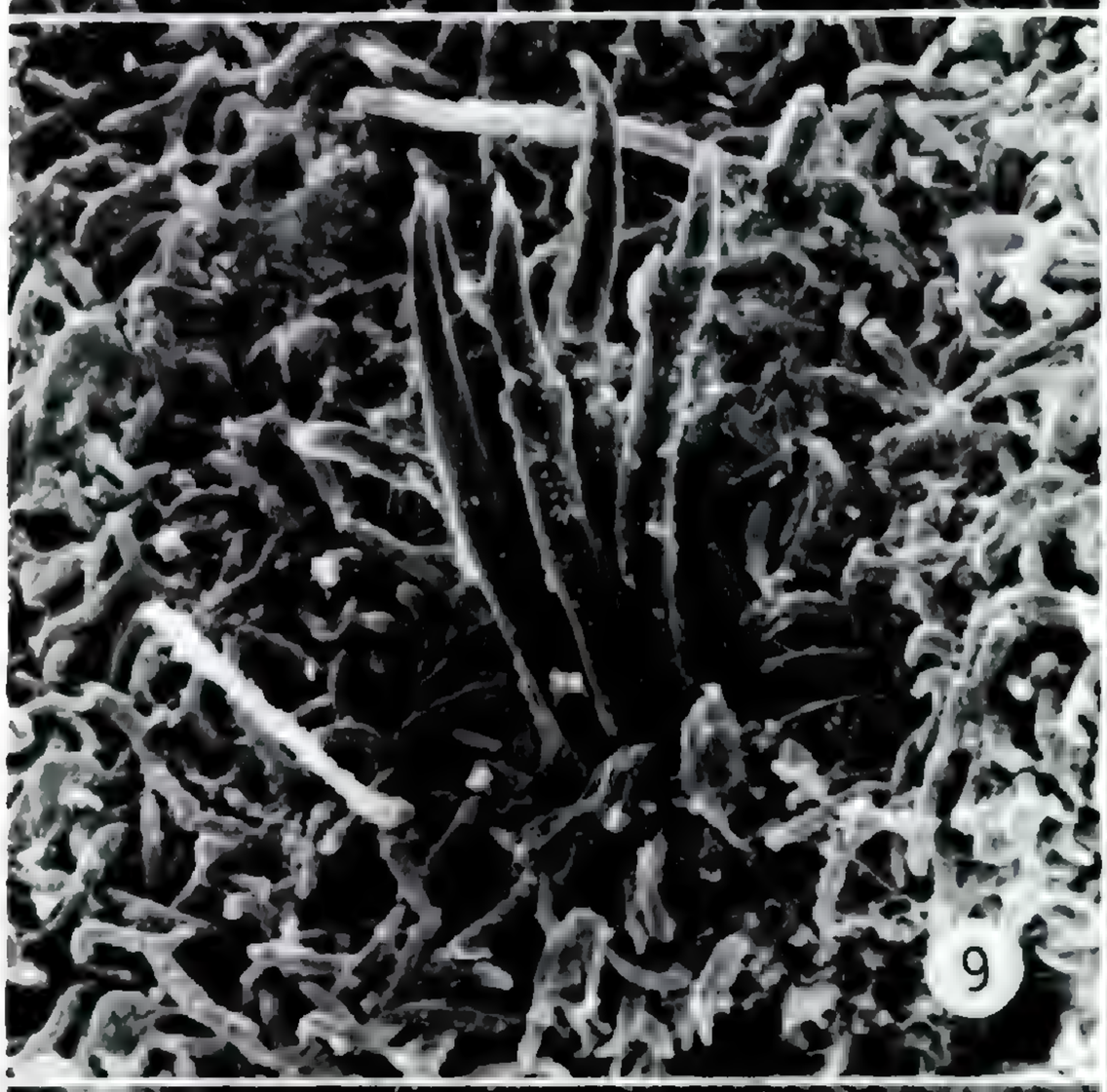
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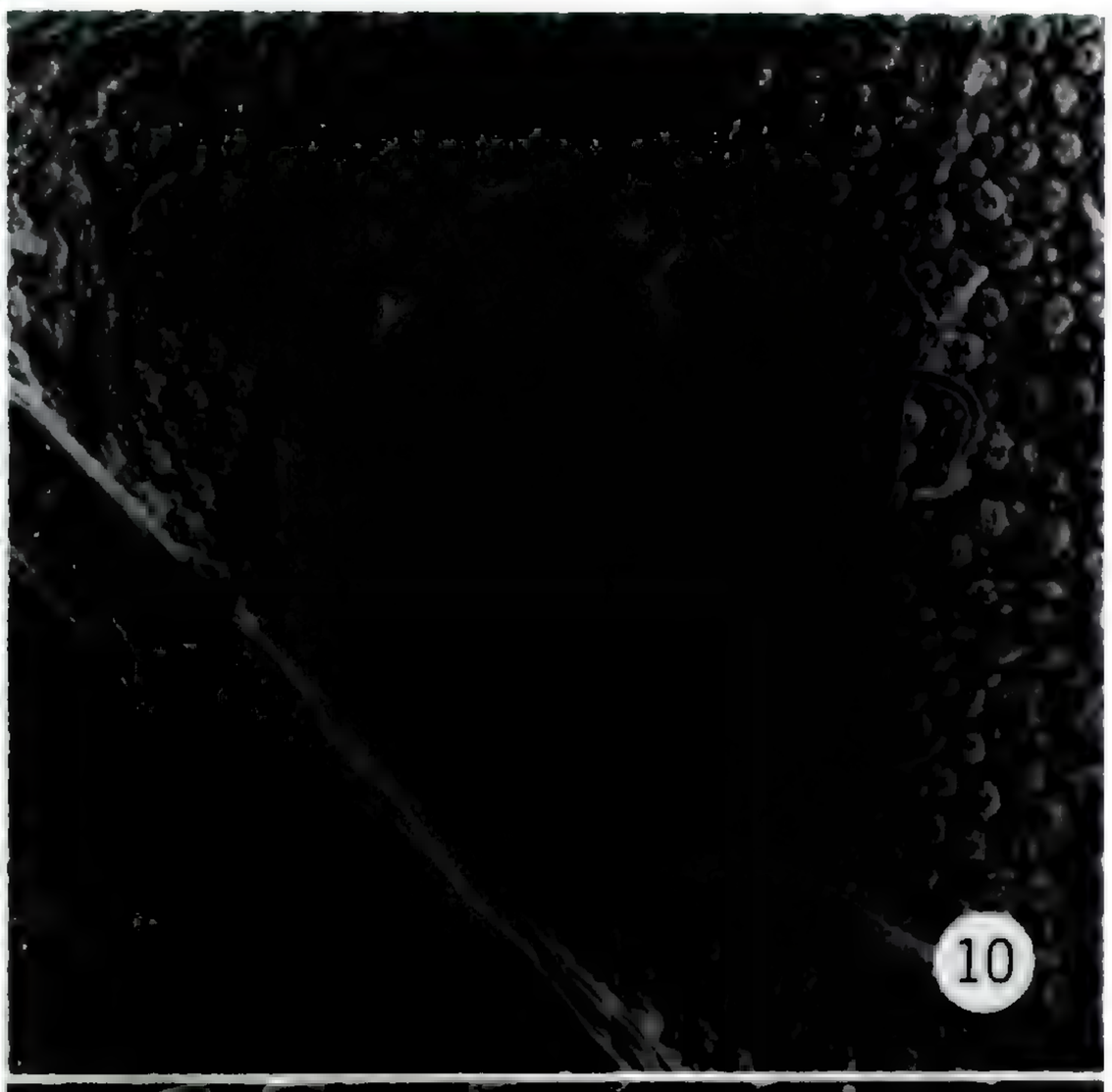
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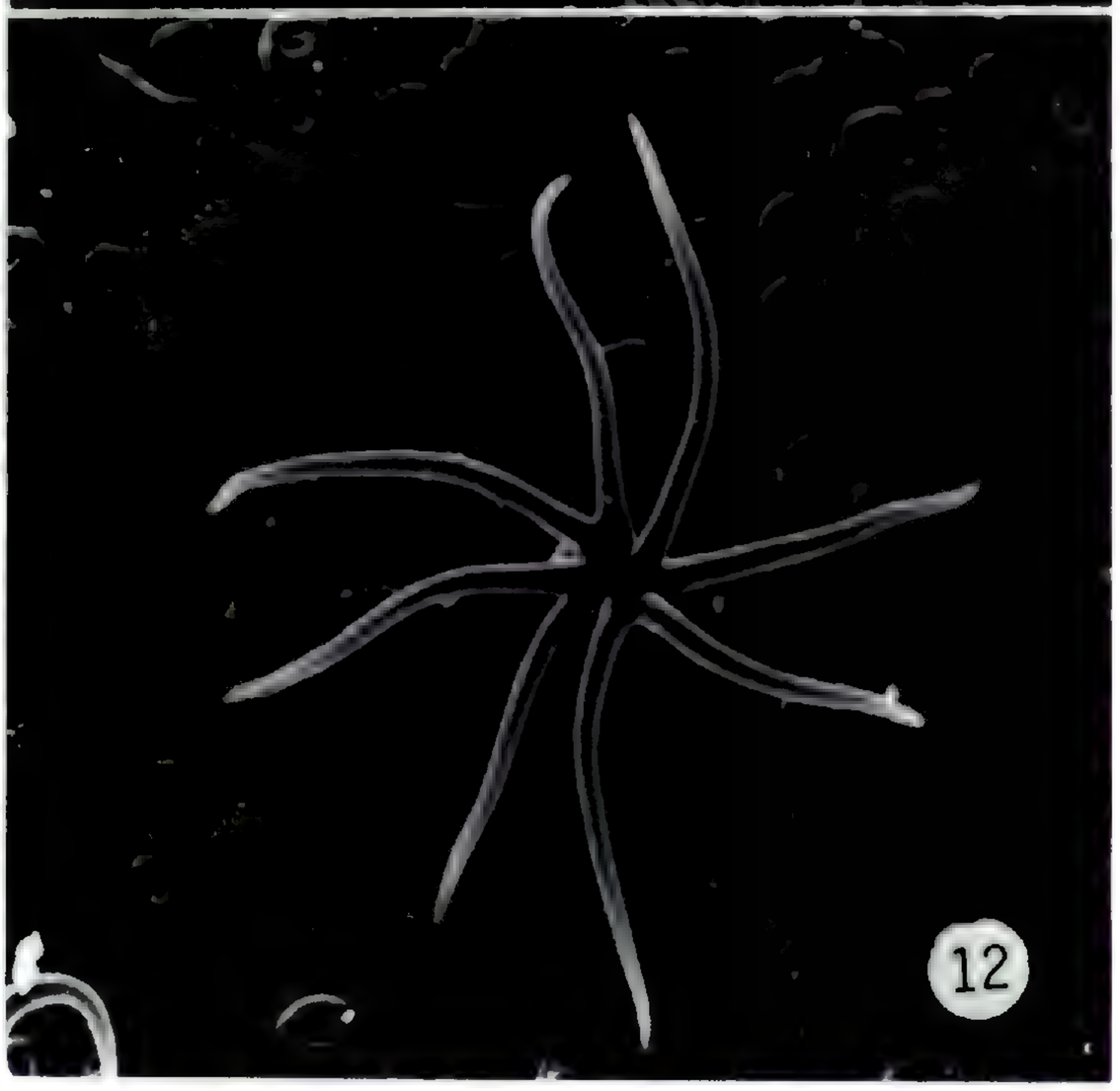
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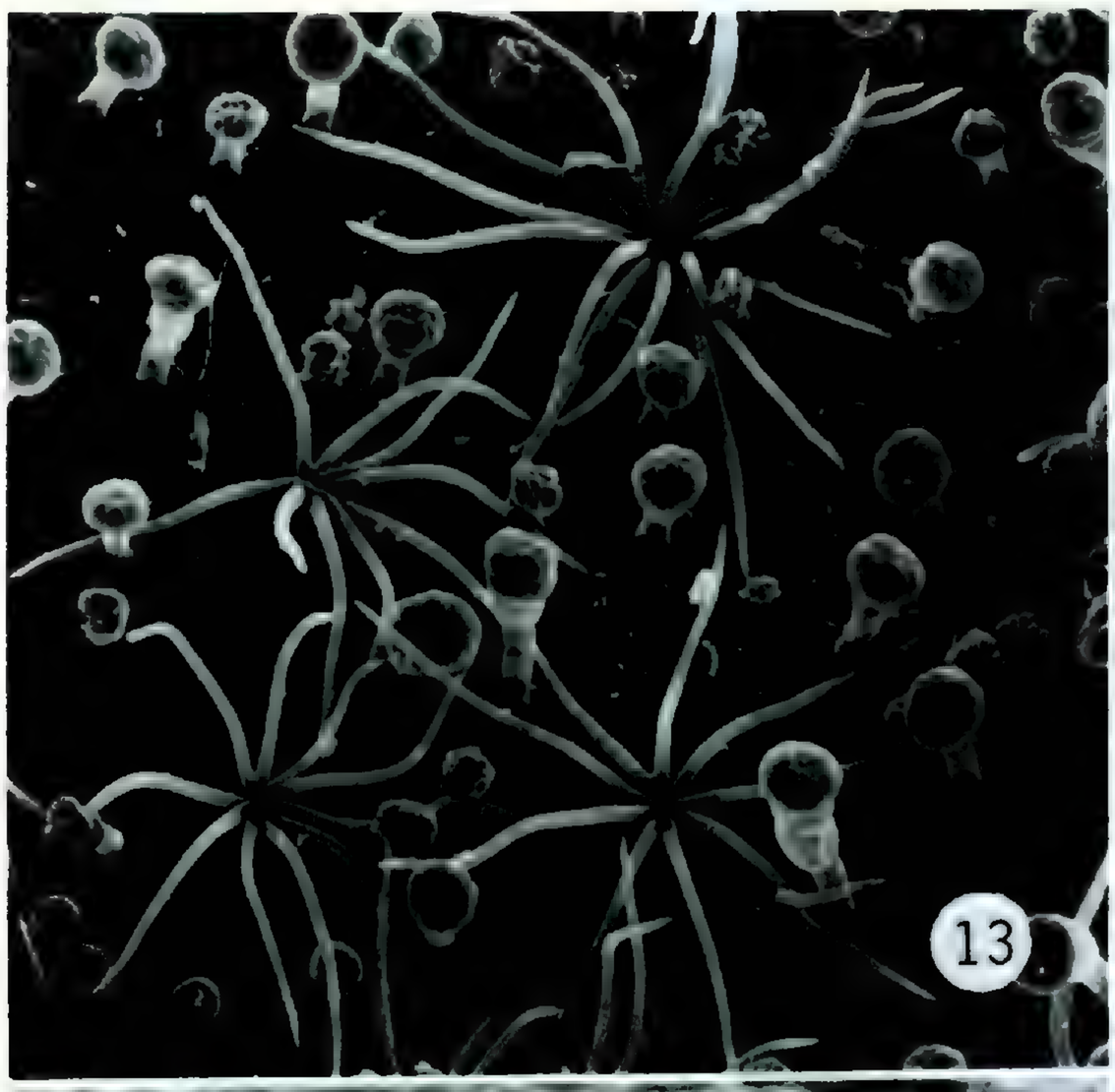
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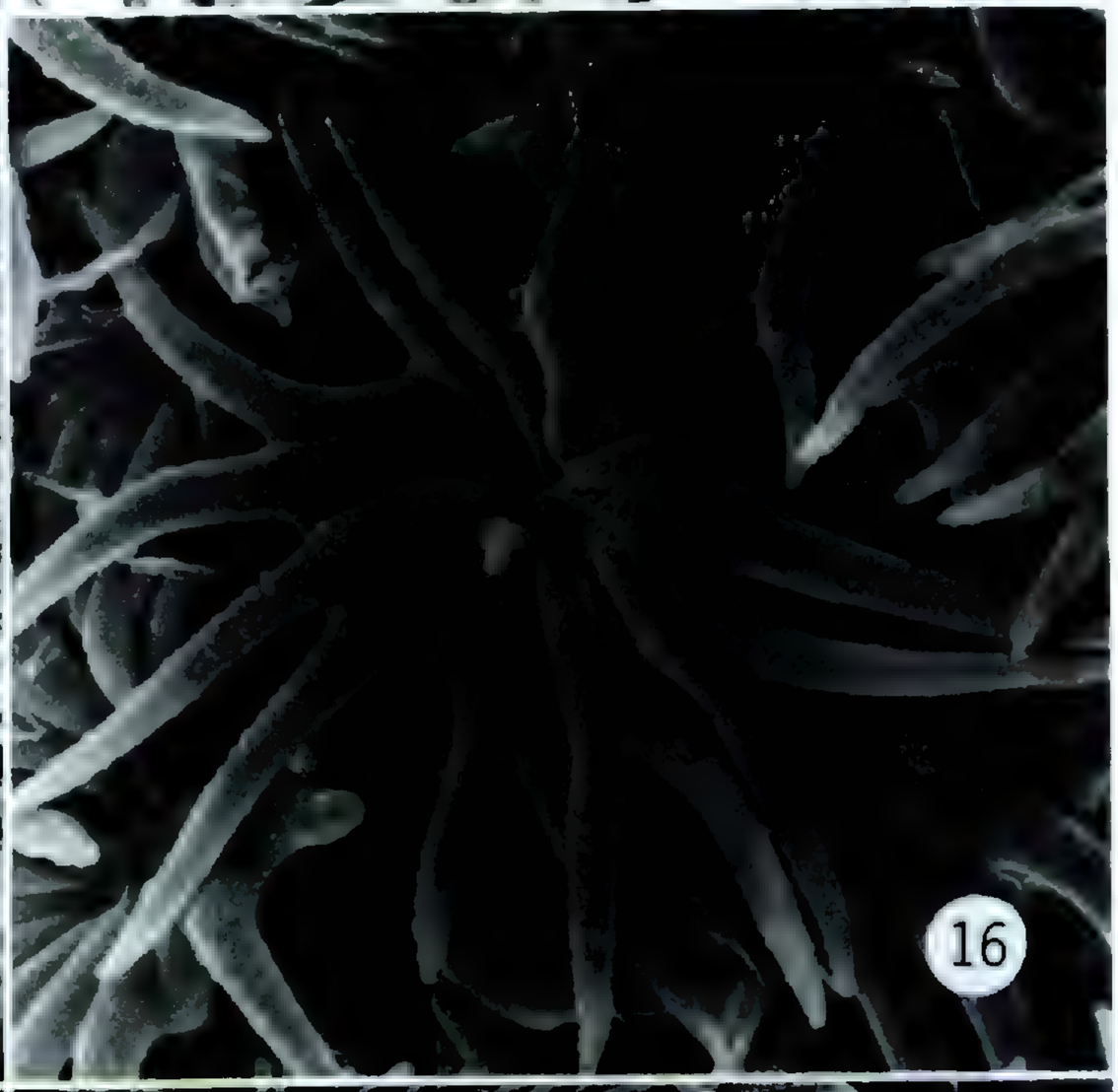
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consists of thin-walled cells. They possess uniseriate stalks and irregularly shaped stellate to discoidal caps composed of many randomly oriented cells (Fig. 33). This type is easily distinguished from type 11 trichomes by the lack of thick cell walls and regular, radially-fused cap cells. They are relatively large and collapse upon drying to form, collectively, a rough mat (Fig. 34). They are extremely difficult to isolate and nearly impossible to distinguish individually by examining whole leaf material. They cover the lower surface of many *Castanopsis* and some *Lithocarpus* species. They are not found outside of the Castaneoideae although some type 19 trichomes (Fig. 53) of *Trigonobalanus* approach this type. When lost they leave round simple bases that give *Castanopsis* cuticles their characteristic speckled appearance (Fig. 35). Camus first (1928–1929) classified these as a "poils tecteurs" but later (1934–1954) discussed them under "poils secreteurs." She called them "poils écailleux ou en ecusson" in the earlier work and "poils en bouclier a pedicelle court" in the latter.

Type 14 (rosulate). These trichomes consist of unicellular, often thin-walled elements, arranged in small bushy tufts (Figs. 36, 37). They are frequently dark in color and have a glistening appearance suggesting glandular function. They intergrade with tufts of types 5 and 10. They generally occur evenly dispersed over the lower surface of the leaf but are occasionally found on the upper surface as well. They are most abundant in the genus *Quercus* but also occur in some species of *Lithocarpus*.

C. "Glandular" trichomes. Trichomes of this group are generally multicellular, apparently glandular in function, and composed of thin-walled cells. Camus (1928–1929, 1934–1954) used the term "poils secreteurs" for trichomes of this type. She did not, for the most part, distinguish the various forms that fall into this category. As Hardin (1976) indicated, this is probably because they intergrade so thoroughly.

Type 15 (simple uniseriate). These trichomes consist of a single column of two or more (generally four or five) thin-walled, apparently glandular cells of nearly equivalent size (Figs. 38, 39). This trichome type intergrades with type 16, which possesses an enlarged terminal cell (or group of cells) or alternatively contains a multiseriate section. The form of type 15 trichomes varies considerably. They may be short and consist of nearly spherical cells, to long and composed of elongate cylindrical cells (Figs. 40, 41). The terminal cells of some forms taper to a point whereas others are rounded and slightly enlarged. When lost, particularly in the preparation of isolated cuticles, they often leave behind a resistant cutinized basal portion (Fig. 42). They are usually distributed evenly over the fine venation on the lower foliar surface. They also are found on the upper surface in many species, but when present they generally occur in much fewer numbers. This is the most basic of the "glandular" types and can be found in all three subfamilies. It reaches its greatest development in the Fagoideae and Quercoideae. Hardin's (1976) type, of the same name, is equivalent.

Type 16 (capitate or irregularly multiseriate). This type consists of a rather heterogeneous group of trichomes, the various forms of which are found together often and intergrade. As envisioned here, type 16 trichomes consist of uniseriate stalks with a single markedly enlarged terminal cell, or a group of terminal cells,

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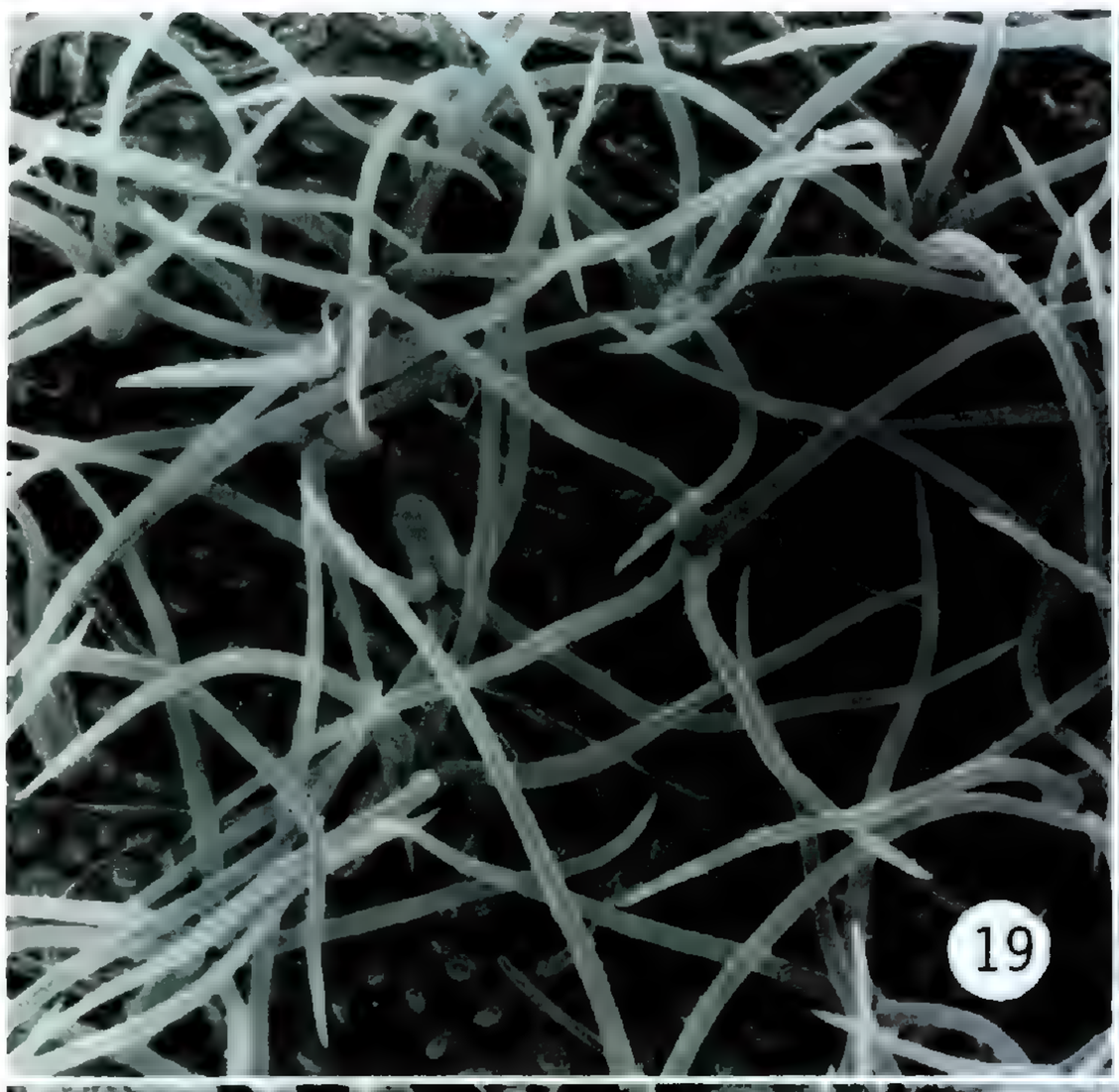
FIGURES 19–24.—19. Scanning electron micrograph of type 8 trichomes scattered over fine veins on the lower leaf surface of *Quercus imbricaria* (3148), 125×.—20. Scanning electron micrograph of type 8 trichomes with long intertwining elements, *Quercus craspopilus* (644), 125×.—21. Photomicrograph of a type 8 trichome with a pedicellate base, lower foliar surface of *Quercus margaretta* (2324), 250×.—22. Scanning electron micrograph of appressed parallel tufts (type 9 trichomes) on the lower leaf surface of *Lithocarpus henryi* (1169), 1,000×.—23. Photomicrograph of type 9 trichomes showing the linear arrangement of elements, lower surface of *Lithocarpus encleisocarpus* (3095), 250×.—24. Scanning electron micrograph of a multiradiate (type 10) trichome on the lower leaf surface of *Quercus emoryi* (617), 250×.

FIGURES 25–30.—25. Scanning electron micrograph of large multiradiate (type 10) trichomes found on the lower leaf surface of *Lithocarpus densiflorus* (492), 125×.—26. Scanning electron micrograph of the rounded base of a large multiradiate trichome from the lower leaf surface of *Lithocarpus densiflorus* (492), 500×.—27. Photomicrograph of a "thick" walled peltate (type 11) trichome characteristic of the genus *Chrysolepis, C. sempervirens* (1207), 650×.—28. Scanning electron micrograph of type 11 trichomes on lower foliar surface of *Chrysolepis chrysophylla* (505), 500×.—29. Scanning electron micrograph showing a dense covering of type 11 trichomes on the lower foliar surface of *Chrysolepis chrysophylla* (505), 125×.—30. Scanning electron micrograph of curly thin walled unicellular (type 12) trichomes covering the lower leaf surface of *Nothofagus solanderi* (3133), 125×.

FIGURES 31–36.—31. Scanning electron micrograph of type 12 trichomes showing basal attachment, *Nothofagus solanderi* (3133), 1,000×.—32. Photomicrograph of type 12 trichomes on the lower surface of a *Nothofagus cliffortioides* (3121) leaf, 250×.—33. "Thin" walled peltate (type 13) trichomes of *Castanopsis* and *Lithocarpus* spp. (redrawn from Camus 1934–1954, 1948), ca. 200×.—34. Scanning electron micrograph of type 13 trichomes on the lower foliar surface of *Castanopsis concinna* (3057), 125×.—35. Photomicrograph of *Castanopsis calathiformis* (3054) showing the characteristic speckled appearance of the lower cuticle produced by type 13 trichome bases, 250×.—36. Scanning electron micrograph of a rosulate (type 14) trichome on the upper leaf surface of *Quercus arkansana* (610), 500×.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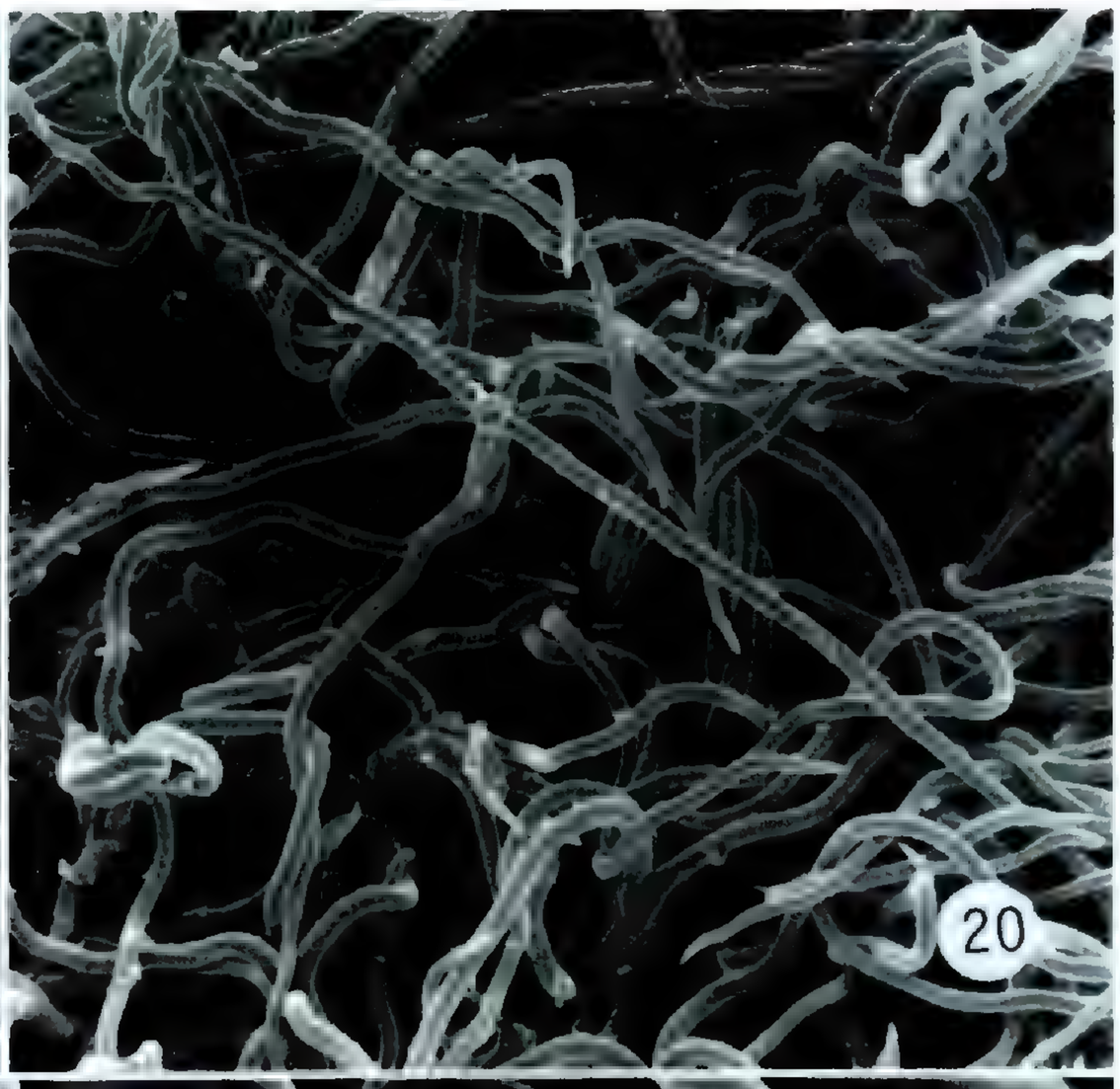
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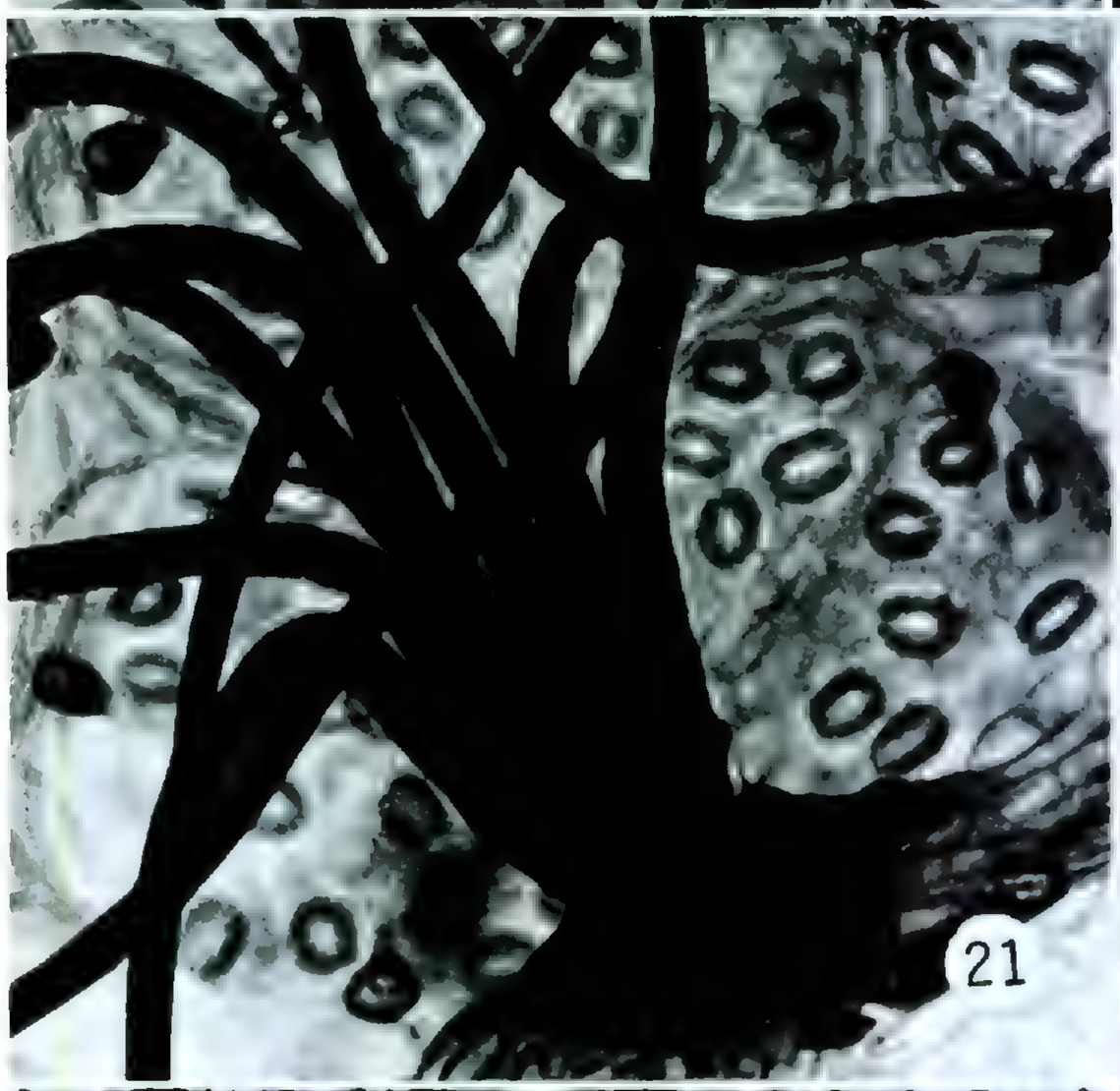
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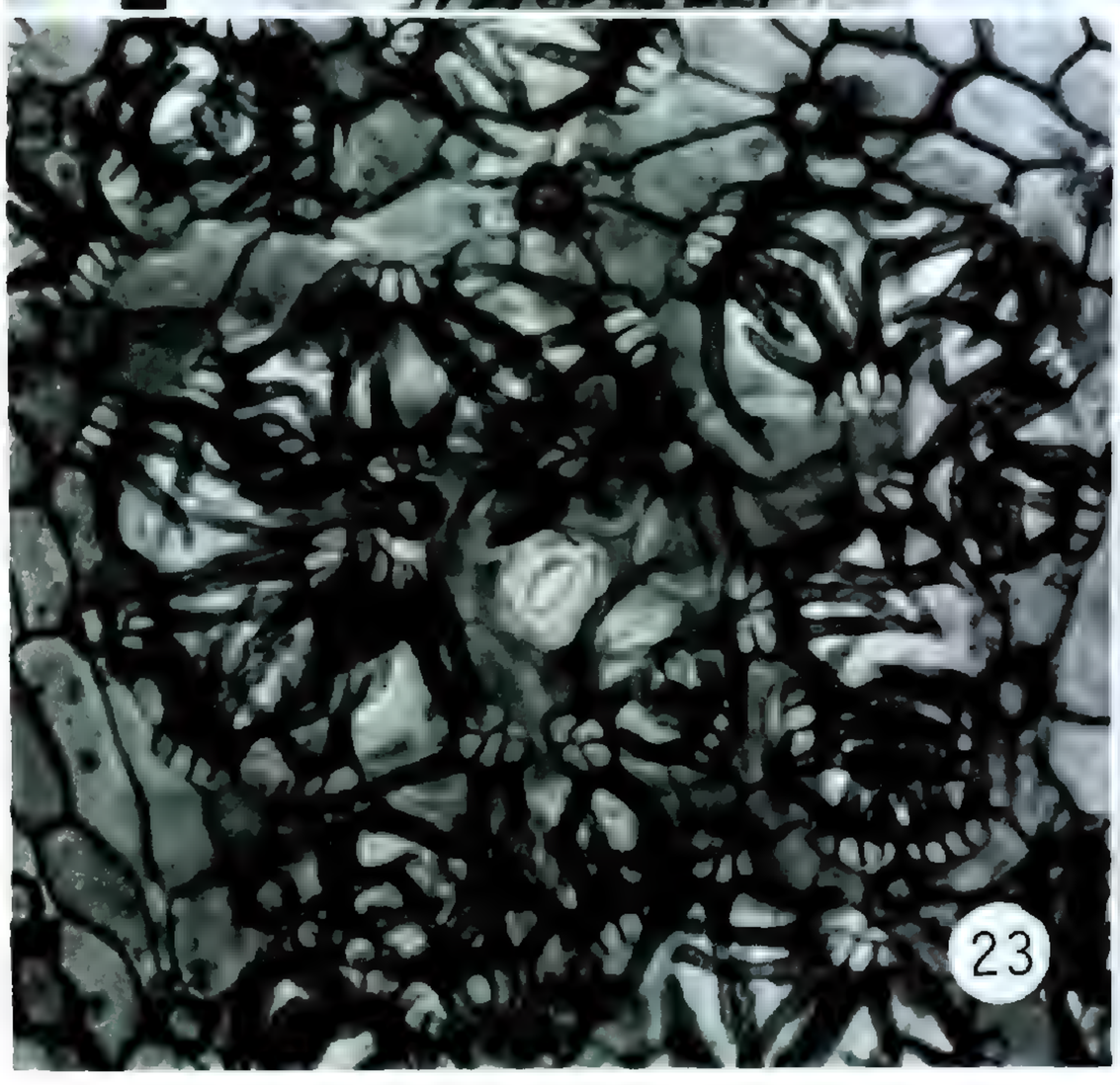
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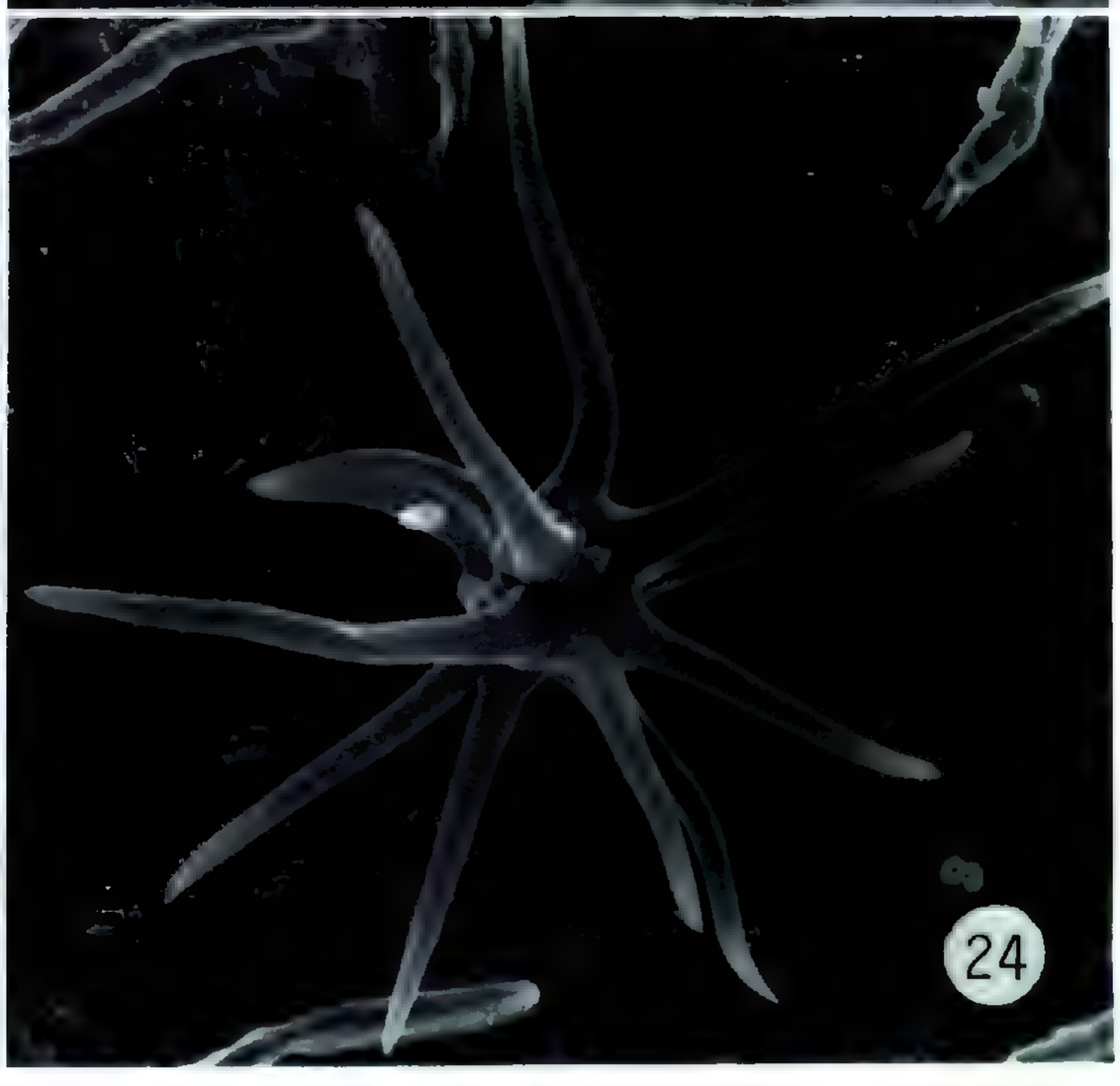
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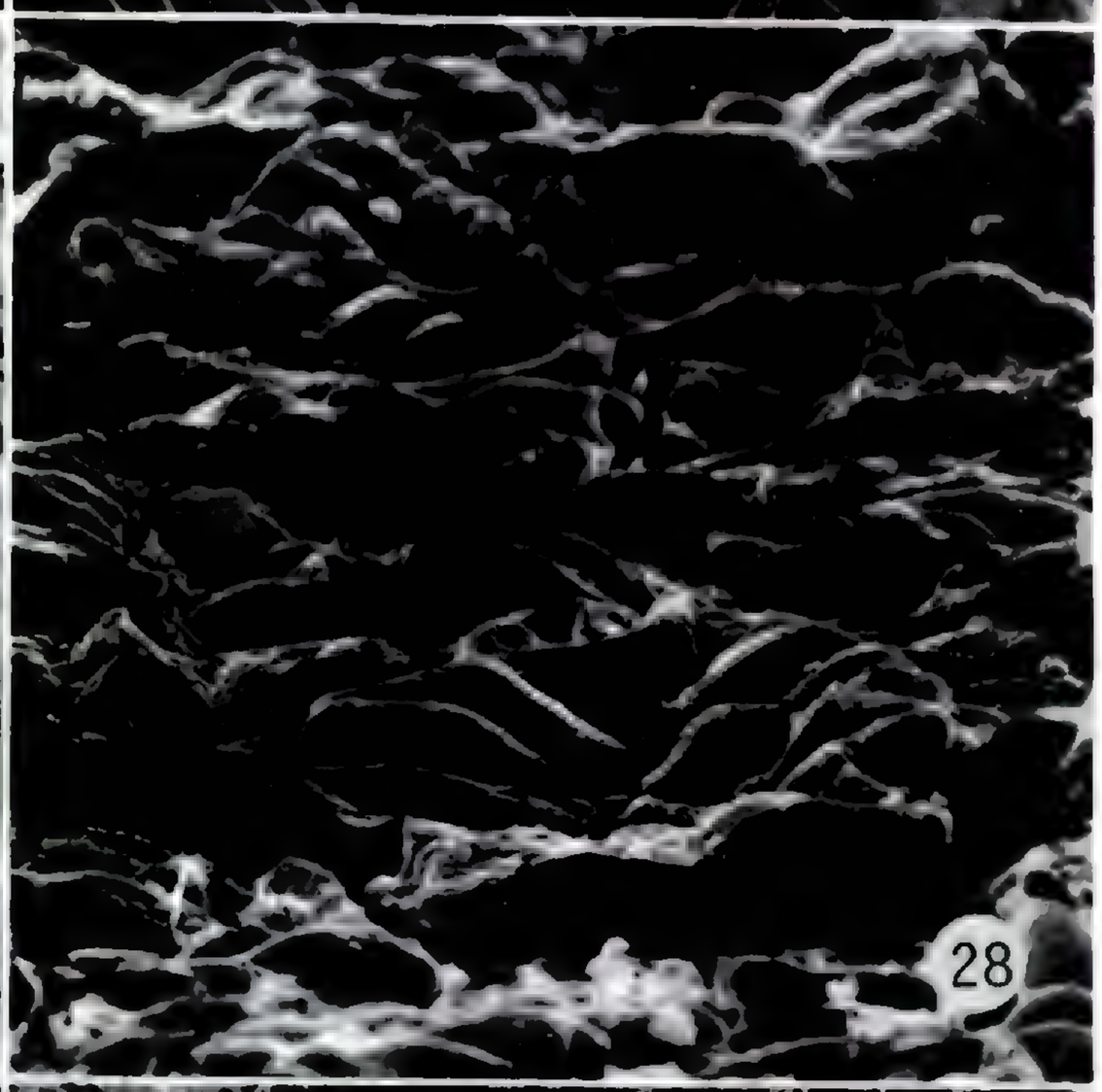
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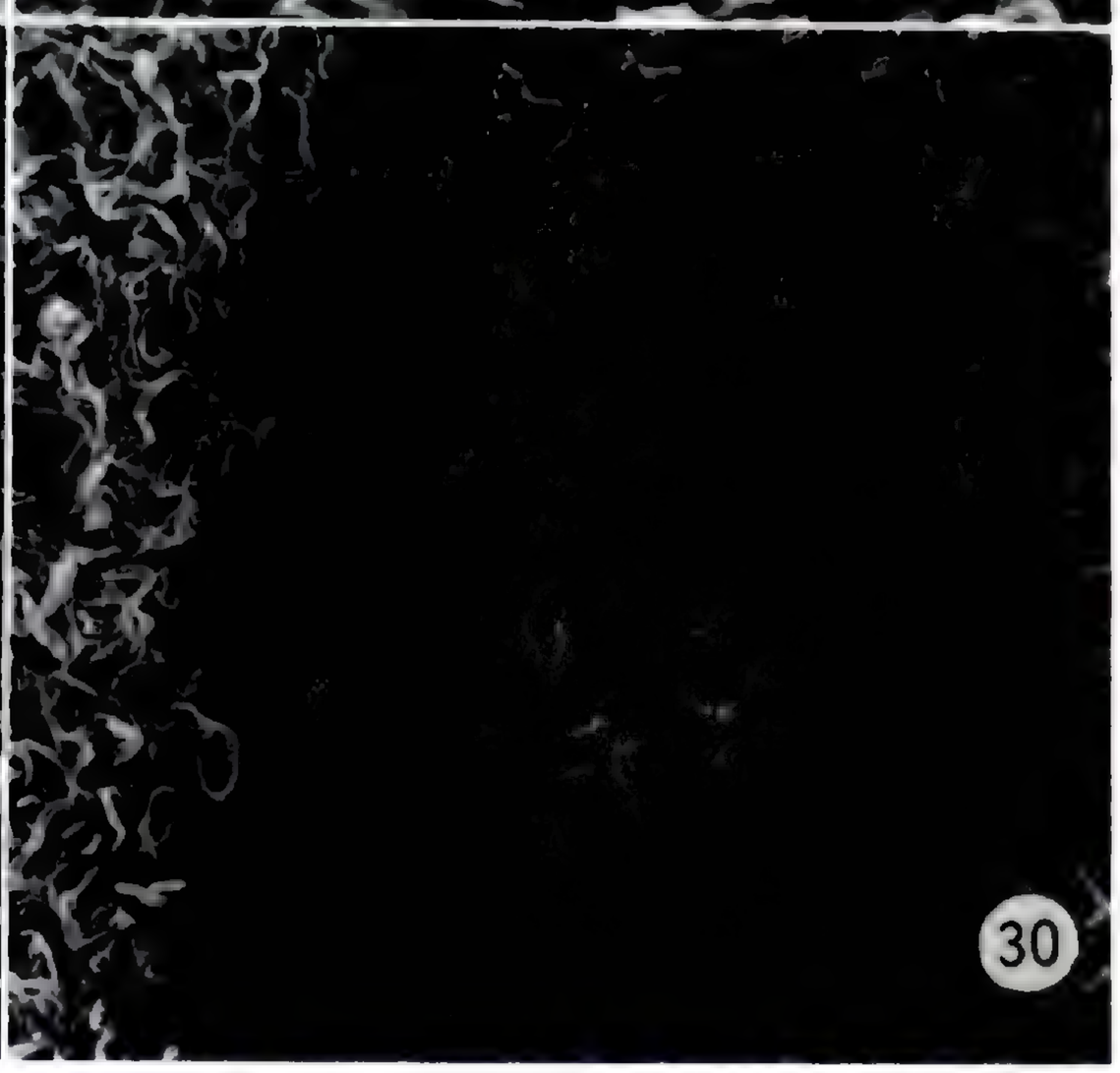
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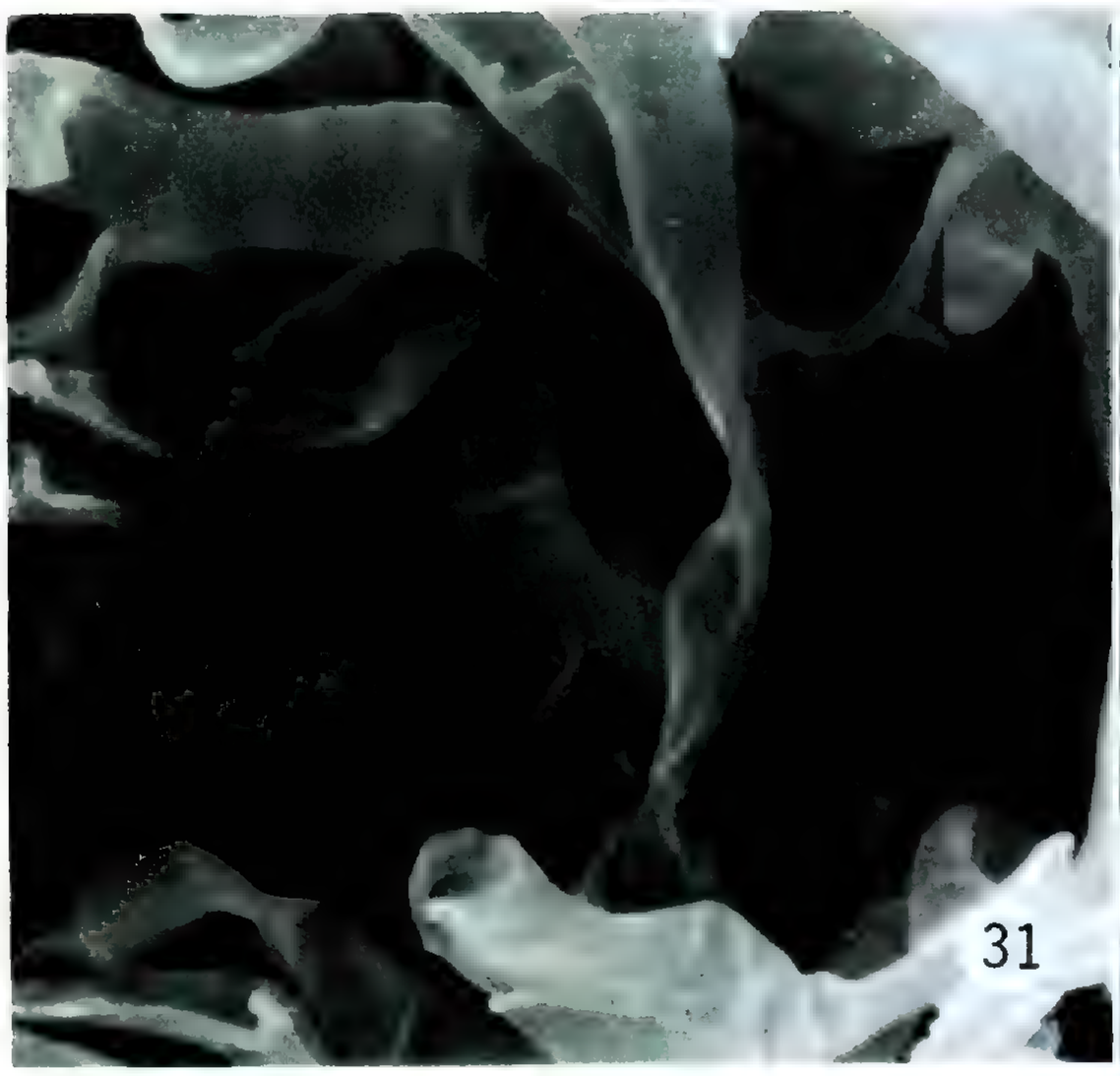
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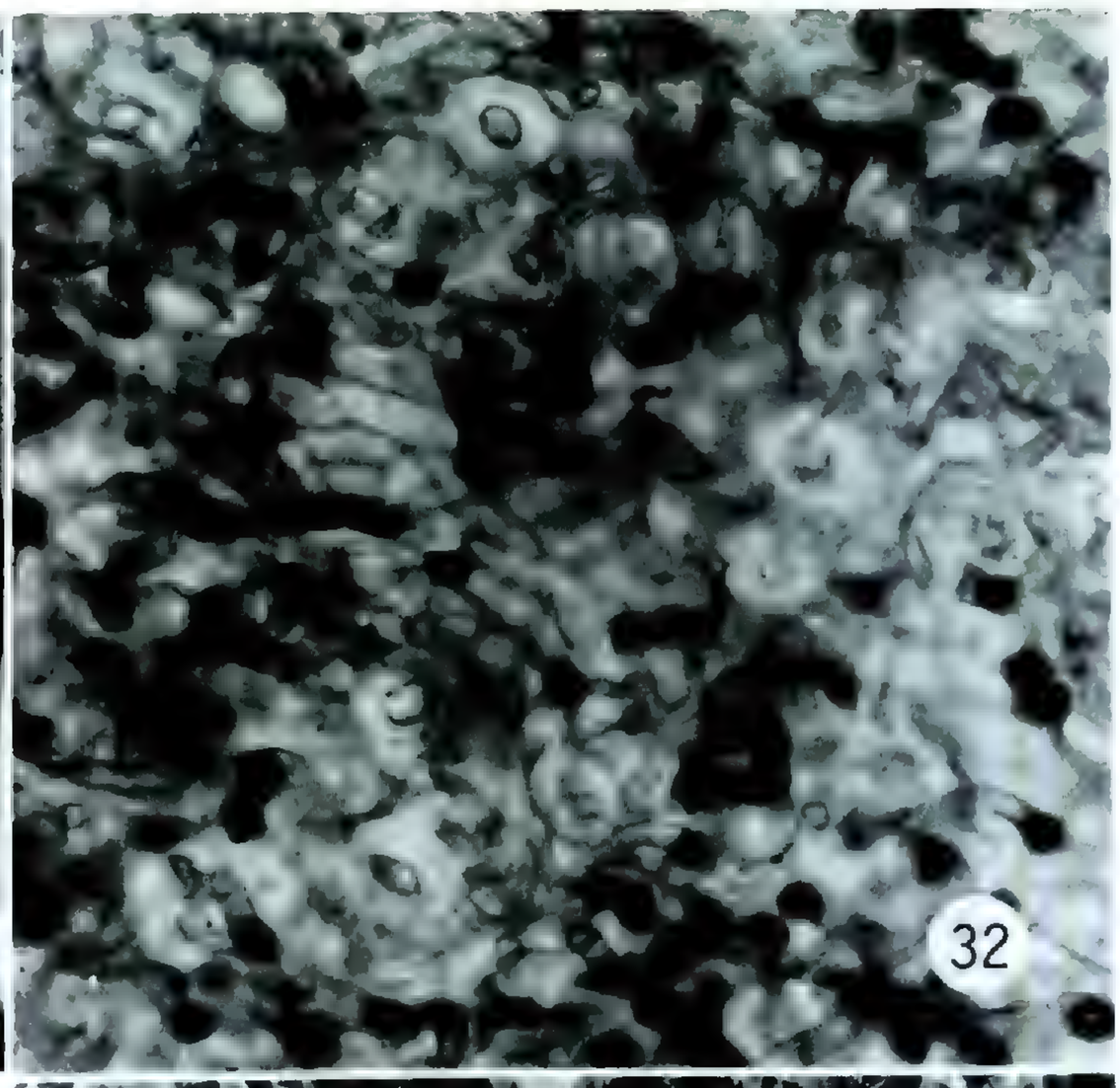
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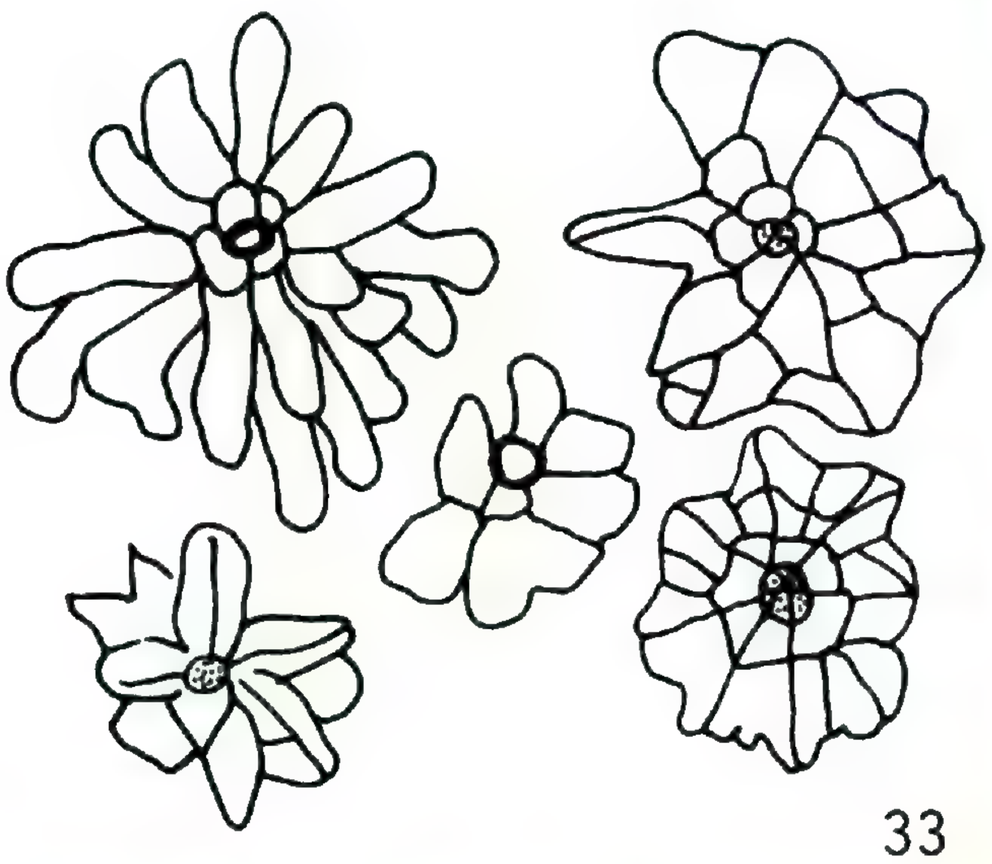
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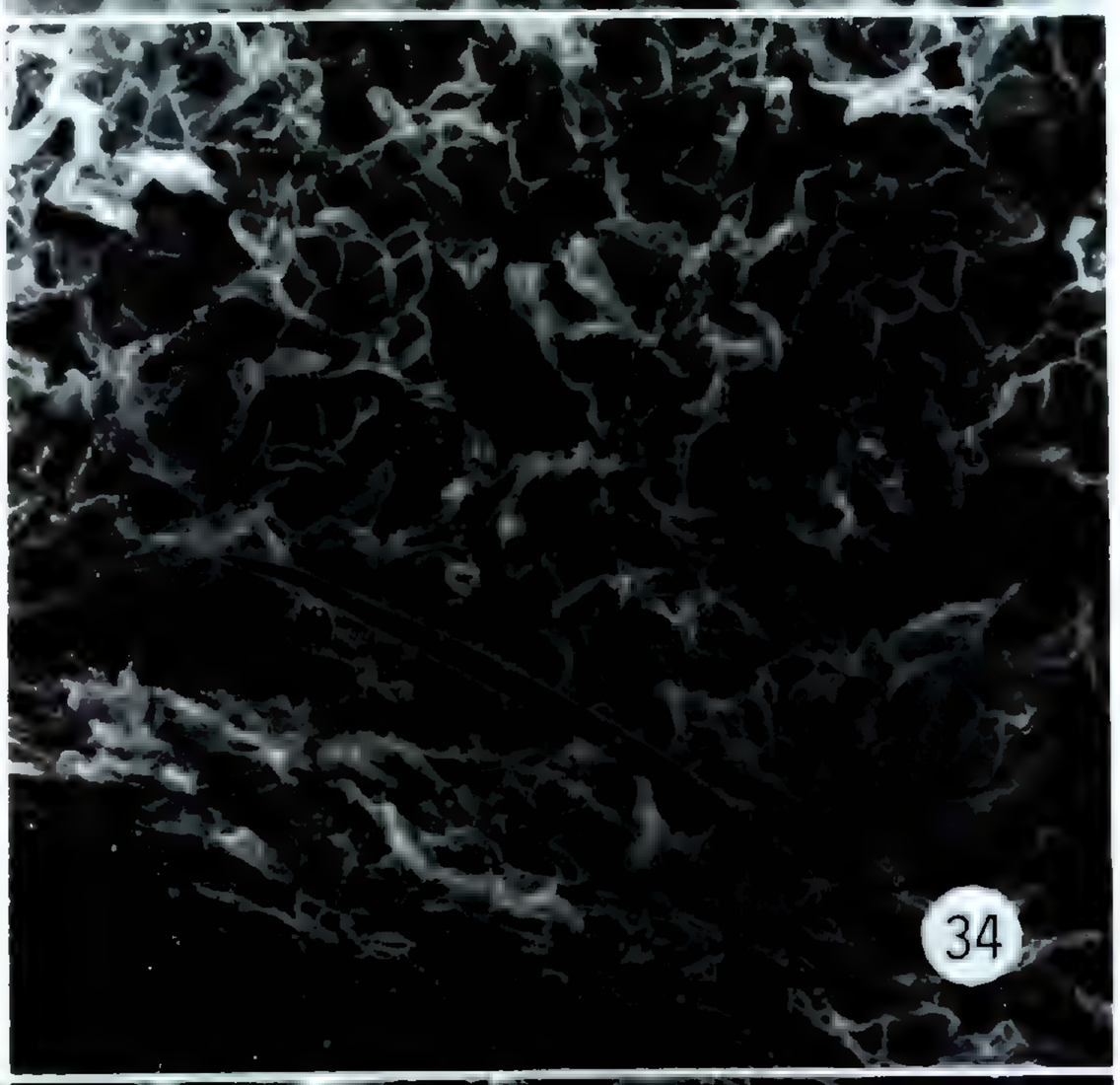
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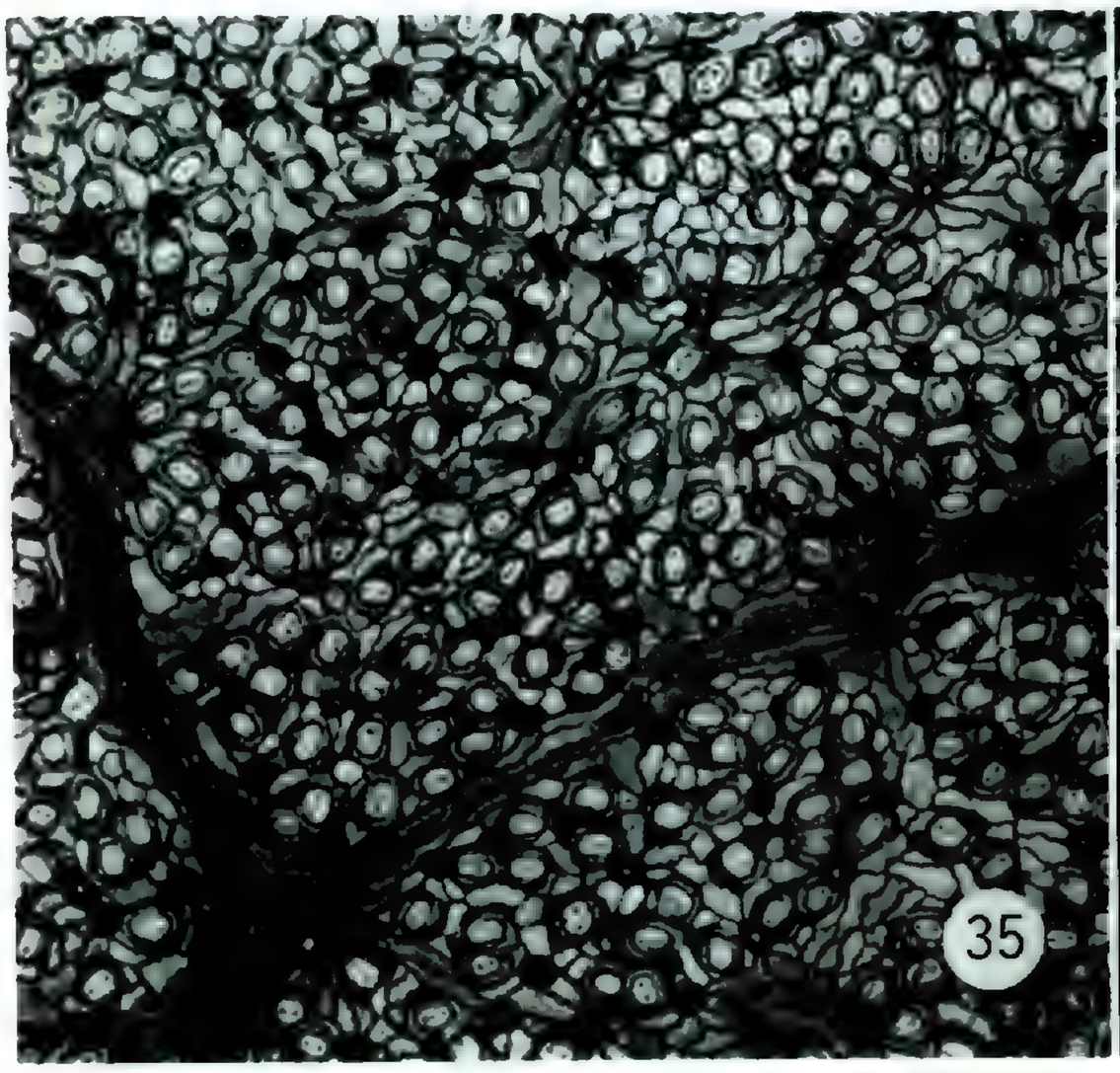
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or, rarely, an intercalary swollen multiseriate section (Figs. 43–45). They are evenly distributed over all orders of venation in young leaves but are often lost with age. In *Quercus* they tend to be more abundant on the upper surface whereas type 15 trichomes are more abundant on the lower. Trichomes of this type are found only in the Quercoideae and Castaneoideae. They reach their maximum development in the genus *Castanea*. Camus (1928–1929) used the term "poil capité" for trichomes of this type. Hardin (1976) called these bulbous trichomes.

Type 17 (large globular). These extremely large trichomes are multicellular and conspicuous. They can be seen with the unaided eye as small dots on the leaf surface (Fig. 46). The component cells are relatively thin-walled, which accounts for the collapse of the structure upon drying (Figs. 47, 48). The stalks are multicellular and leave large scars in the cuticle when lost (Fig. 49). They appear to be glandular in function and may produce the sticky coating characteristic of young *Nothofagus* leaves. These trichomes occur widely scattered over the fine venation on both sides of the leaf. Like most trichomes, they are more abundant on the lower surface, particularly in the tropical species. Large globular trichomes are restricted to *Nothofagus,* in which they can be found in all but a few species.

Type 18 (branched uniseriate). These trichomes are similar to type 15 in cellular composition. They are different from those of type 15 in that they branch at least once (Fig. 50). Branching sometimes results in a nearly equal dichotomy, but more frequently it is irregular and produces a large number of oddly shaped forms (Figs. 51, 52). The cells are often colored and appear to bear or contain secretory substances. This trichome type intergrades with types 13 and 19. It occurs in the Castaneoideae and Quercoideae, with greatest development occurring in *Lithocarpus*. Trichomes of this type are classified as "simple branched" by Hardin (1976).

Type 19 ("glandular" peltate). These trichomes have cell walls of moderate thickness and a reddish brown glistening appearance. The sheen and color suggest a glandular function although there is no direct evidence to confirm this. This trichome type thoroughly intergrades with type 18 trichomes found on the same leaf (Figs. 51, 53, 54). Type 19 trichomes are found only in *Trigonobalanus doichangensis*. They lack the regularity of type 11 trichomes. This type can be distinguished from type 13 trichomes by its thicker cell walls and darker color. Camus (1934–1954) classified these trichomes as "poils en e'cusson."

Septate trichomes very similar to those of types 1 and 5 have been reported by Camus (1928–1929, pl. 14:19, 1934–1954, pl. 61:19). The "crosswalls" are not nearly as thick as the side walls. There is no indication of glandular function. In many cases, apparent crosswalls, which may represent the "degenerative membrane thickenings" of Kuester or simply cytoplasmic debris, can be found in unicellular elements. Truly septate trichomes are very rare and have been reported by Camus (1928–1929, 1934–1954) only in the genera *Castanopsis* and *Quercus*. They have also been observed by the author on floral structures of *Chrysolepis*.

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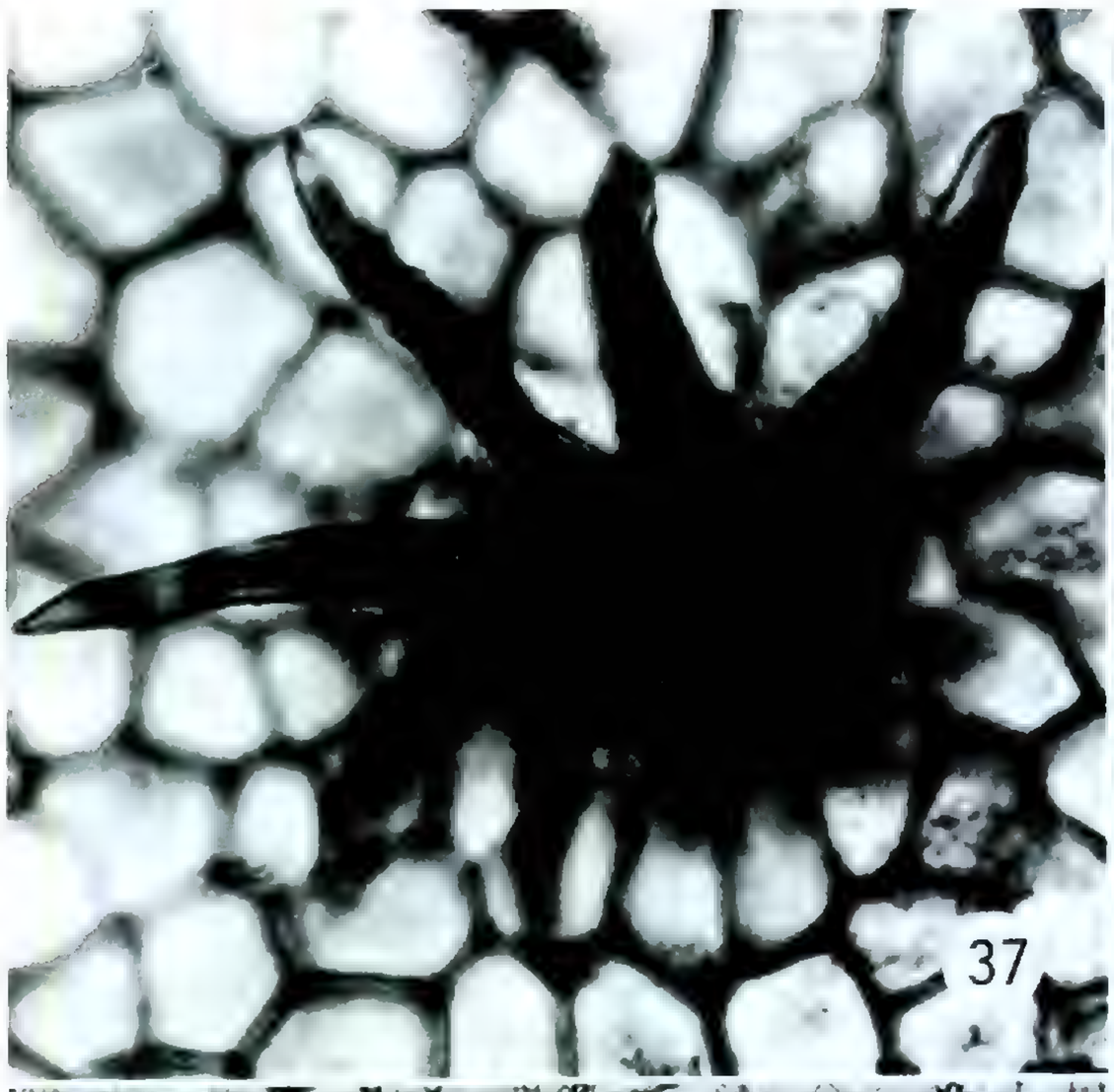
FIGURES 37–42.—37. Photomicrograph of a type 14 trichome on the upper cuticle of *Lithocarpus cooperta* (3091), 650×.—38. Scanning electron micrograph of a simple uniseriate (type 15) trichome on the lower leaf surface of *Quercus atriglans* (144), 500×.—39. Photomicrograph of type 15 trichomes on the lower leaf surface of *Quercus schottkyana* (1186), 250×.—40. Scanning electron micrograph of a short type 15 trichome composed of spherical cells, lower leaf surface of *Quercus adenonerva* (132), 500×.—41. Scanning electron micrograph of a long type 15 trichome composed of elongate cylindrical cells, lower surface of a *Quercus acutissima* (1170) leaf, 250×.—42. Photomicrograph of the resistant basal portions of type 15 trichomes on the lower cuticle of a *Quercus acutissima* (1170) leaf, 250×.

FIGURES 43–48.—43. Scanning electron micrograph of capitate (type 16) trichomes on the upper surface of a *Castanea crenata* (A1) leaf, 500×.—44. Photomicrograph of a type 16 trichome from the lower cuticle of *Castanea sativa* (114), 250×.—45. Drawings of type 16 trichomes, many with intercalary multiseriate sections, *Quercus* spp. (redrawn from Camus, 1934–1954, 1938), ca. 200×.—46. *Nothofagus bernhardi* (3118) leaf showing large globular (type 17) trichomes scattered over the lower surface, 2×.—47. Scattered electron micrograph of a collapsed type 17 trichome on the lower surface of a *Nothofagus betuloides* (3119) leaf, 250×.—48. Scanning electron micrograph of type 17 trichomes scattered among type 2 trichomes on the lower surface of a *Nothofagus antarctica* (3117) leaf, 125×.

FIGURES 49–54.—49. Photomicrograph of a type 17 trichome base on the lower cuticle of *Nothofagus aequilateralis* (3587), 250×.—50. Scanning electron micrograph of branched uniseriate trichomes on the lower epidermis of a *Quercus palmeri* (3141) leaf, 125×.—51. Scanning electron micrograph of type 18 trichomes on the lower epidermis of *Trigonobalanus doichangensis* (1330), 500×.—51. Drawings of type 18 trichomes from *Quercus* and *Lithocarpus* spp. (redrawn from Camus, 1934–1954, 1948), ca. 100×.—53. Scanning electron micrograph of a "glandular" peltate (type 19) trichome on the upper epidermis of *Trigonobalanus doichangensis* (1330), 500×.—54. "Glandular" peltate trichomes of *Trigonobalanus doichangensis* (redrawn from Camus, 1934–1954 and Cutler, 1964), ca. 100× (smaller 2) and 160× (larger 2).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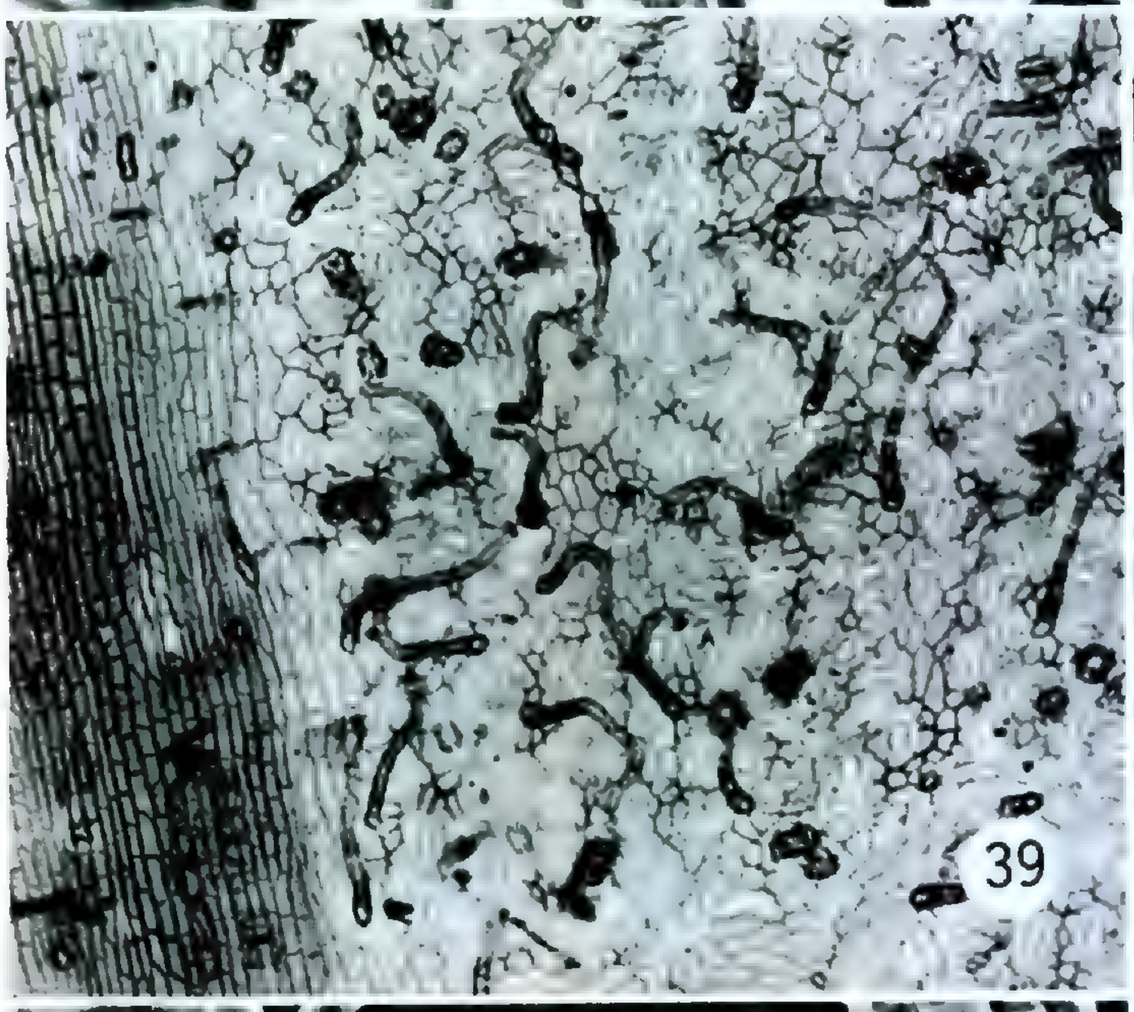
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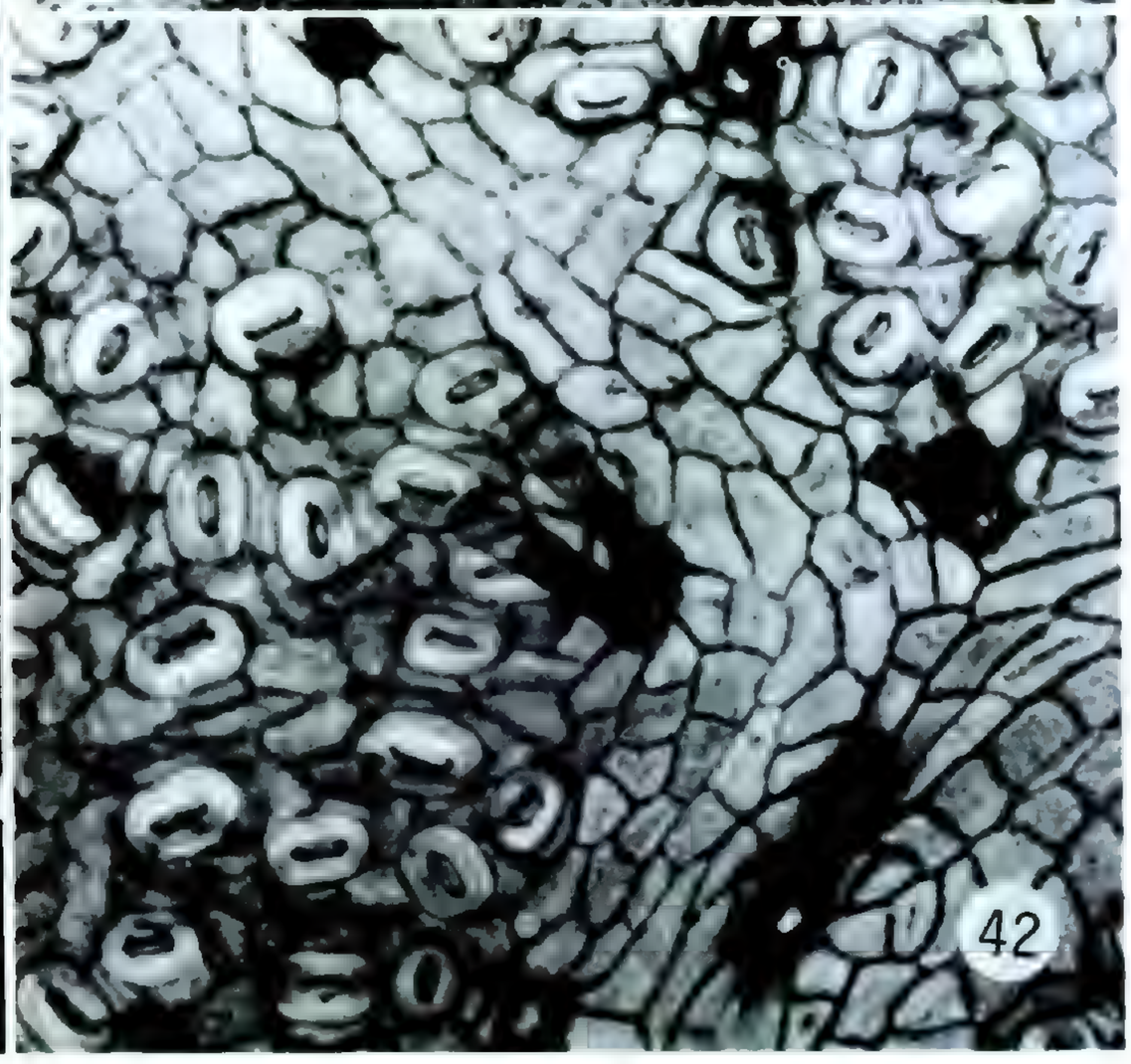
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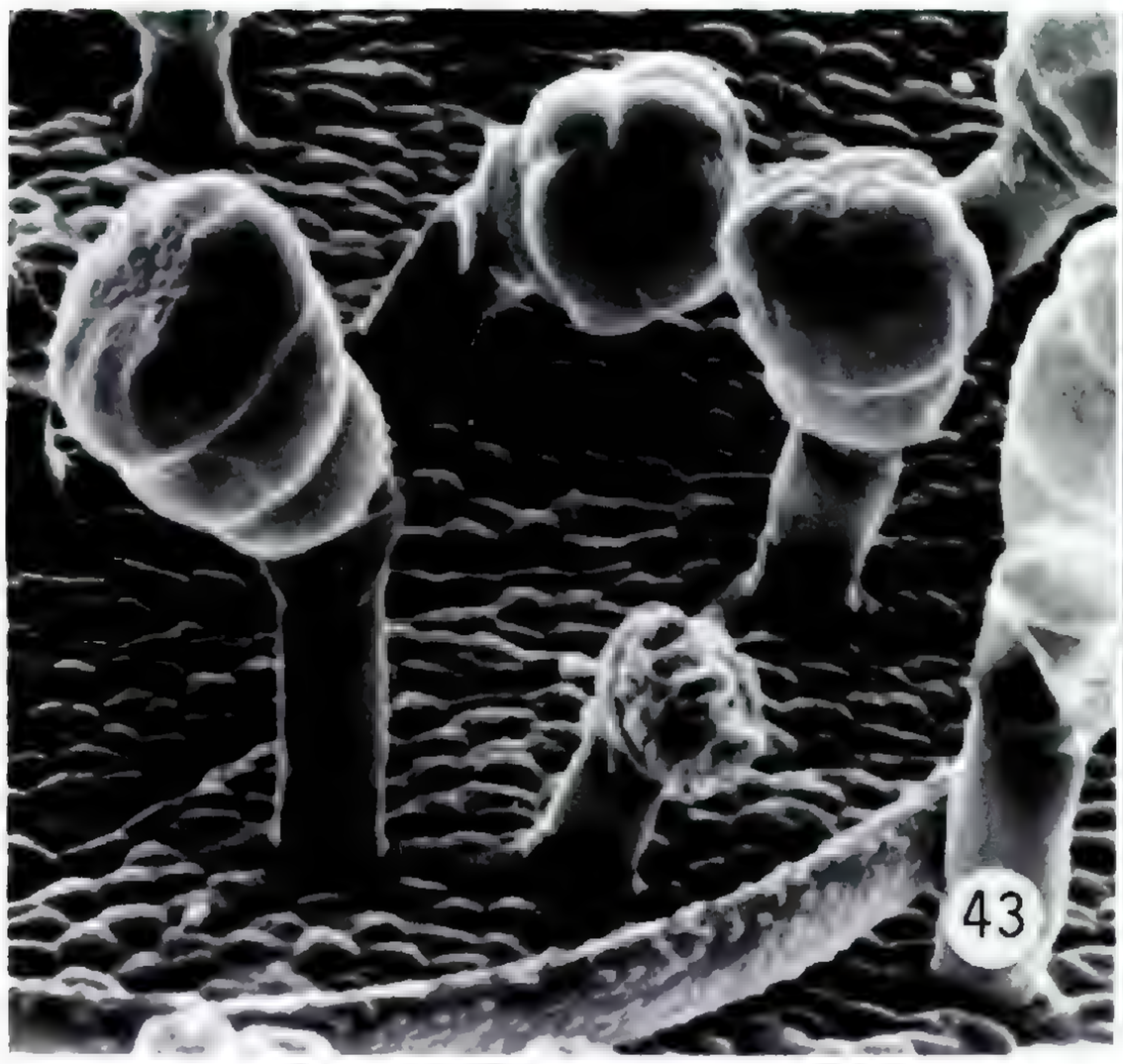
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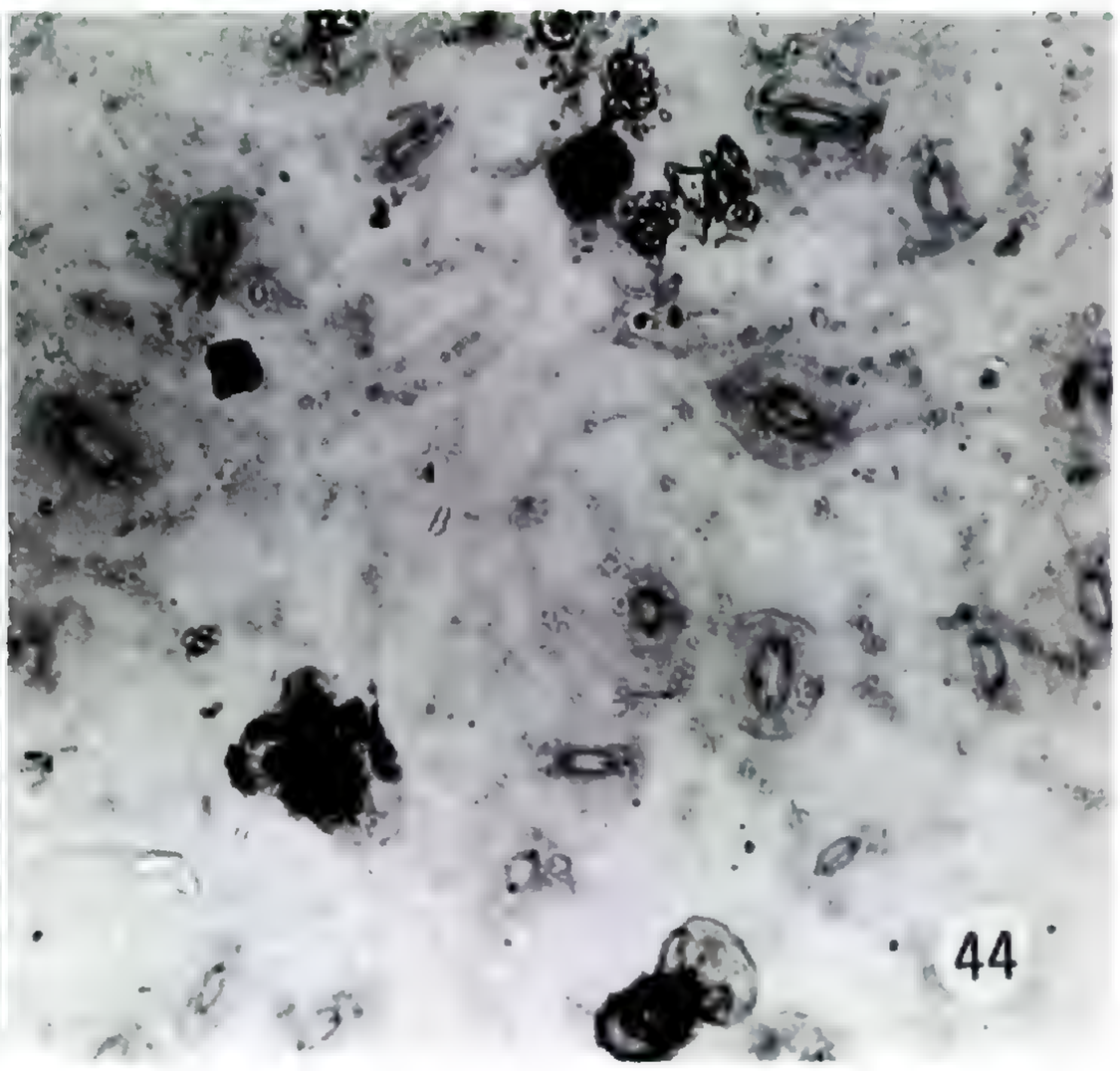
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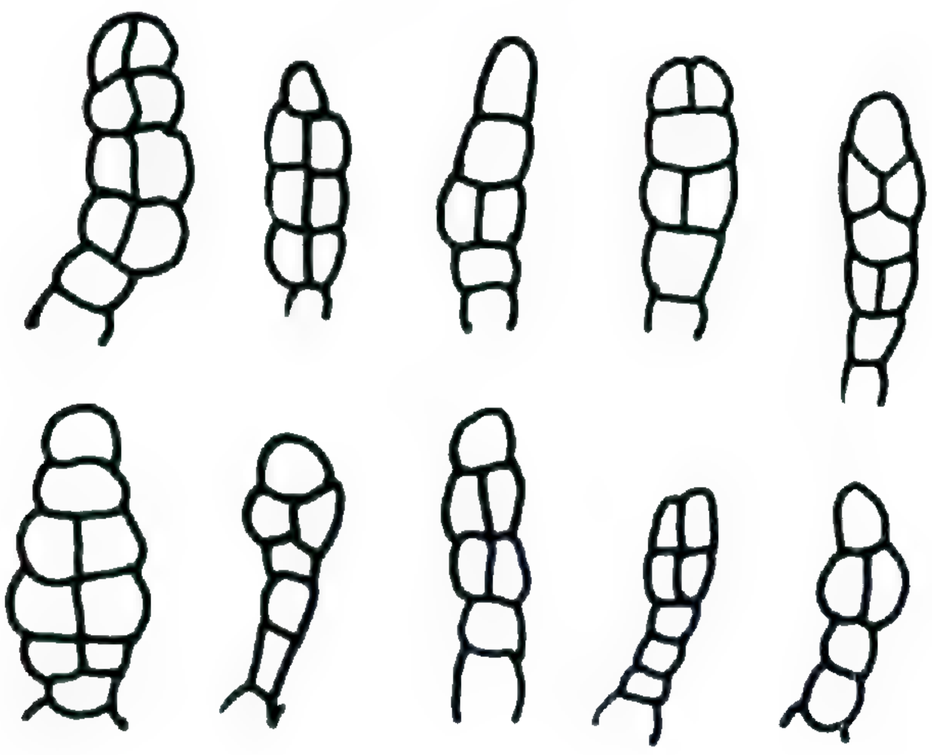
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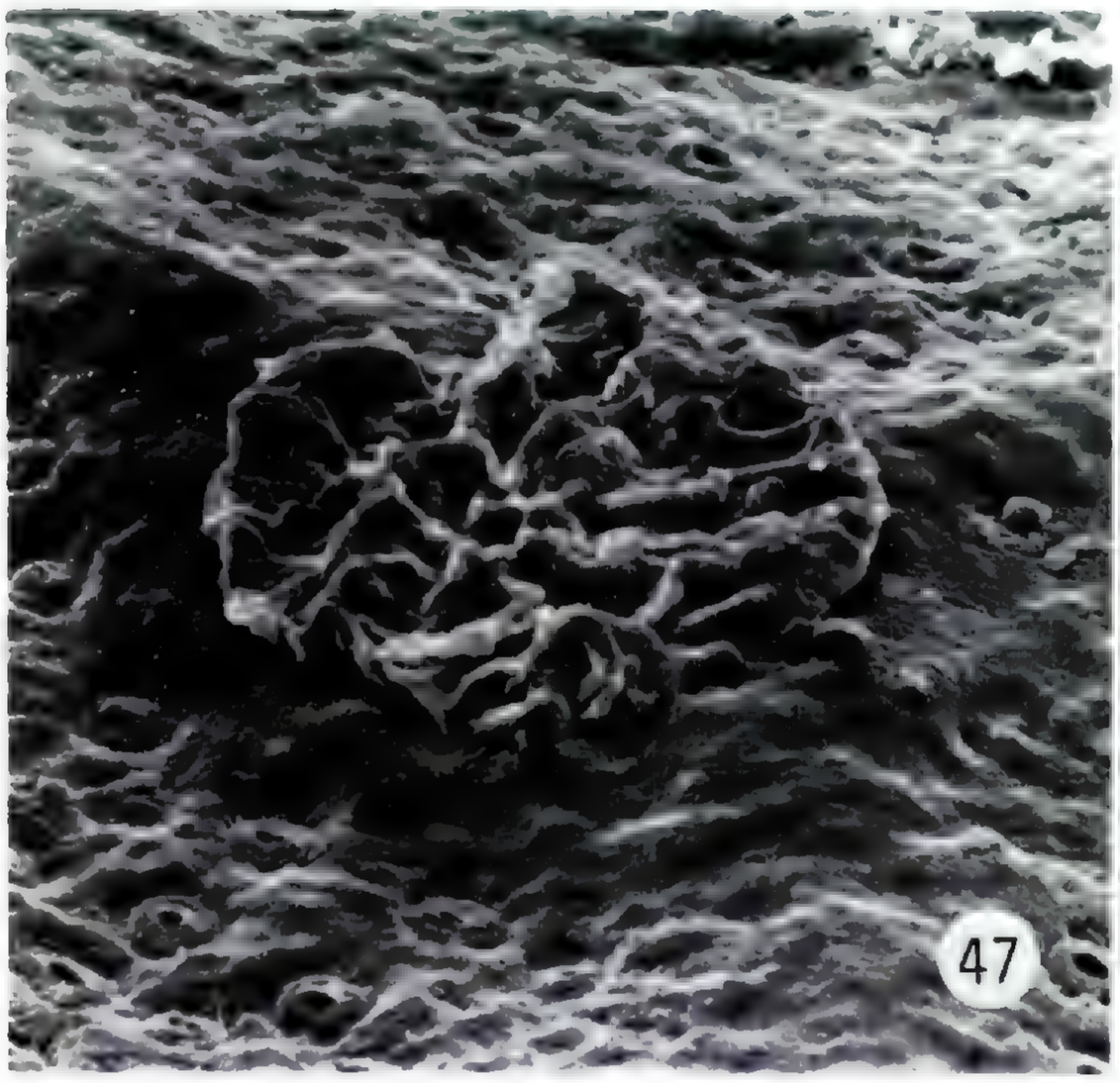
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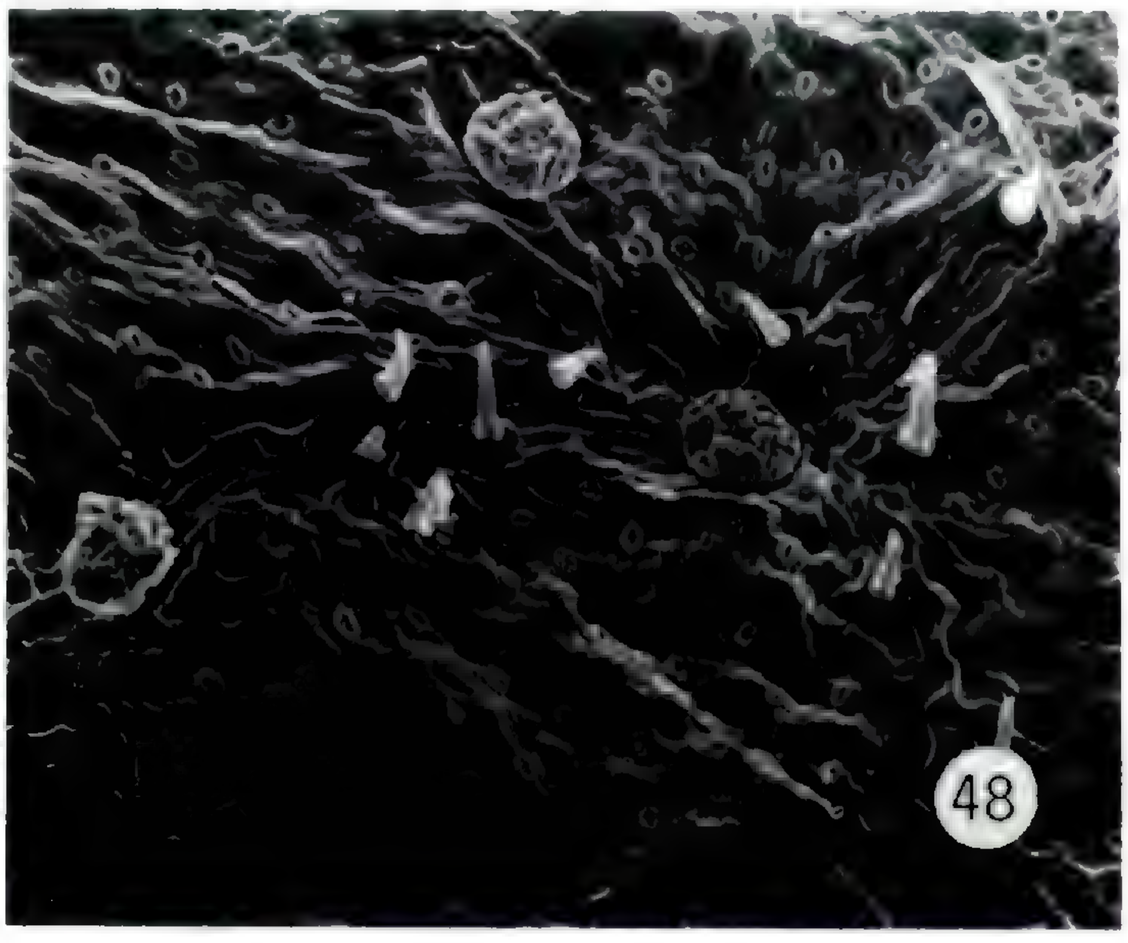
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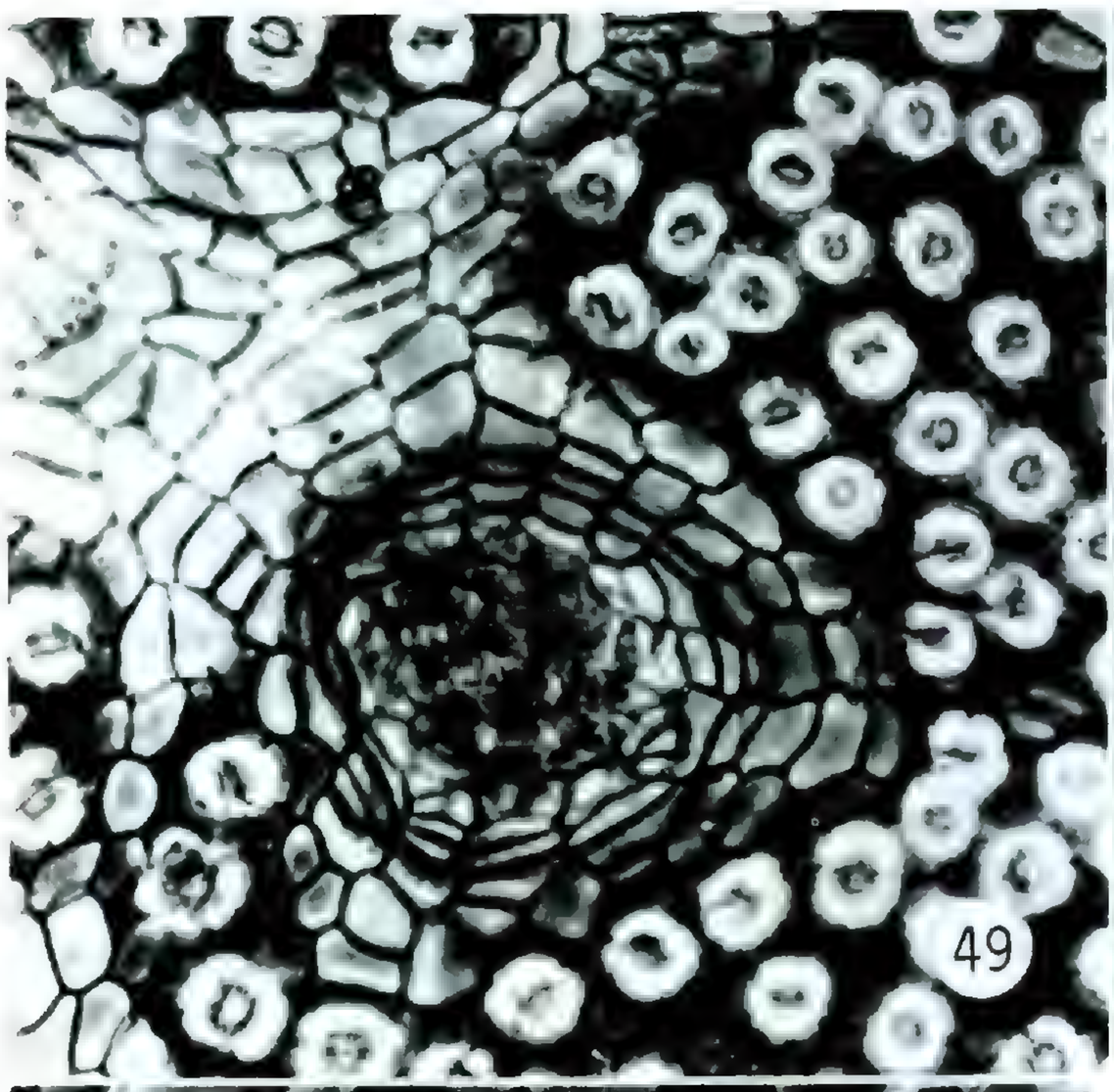
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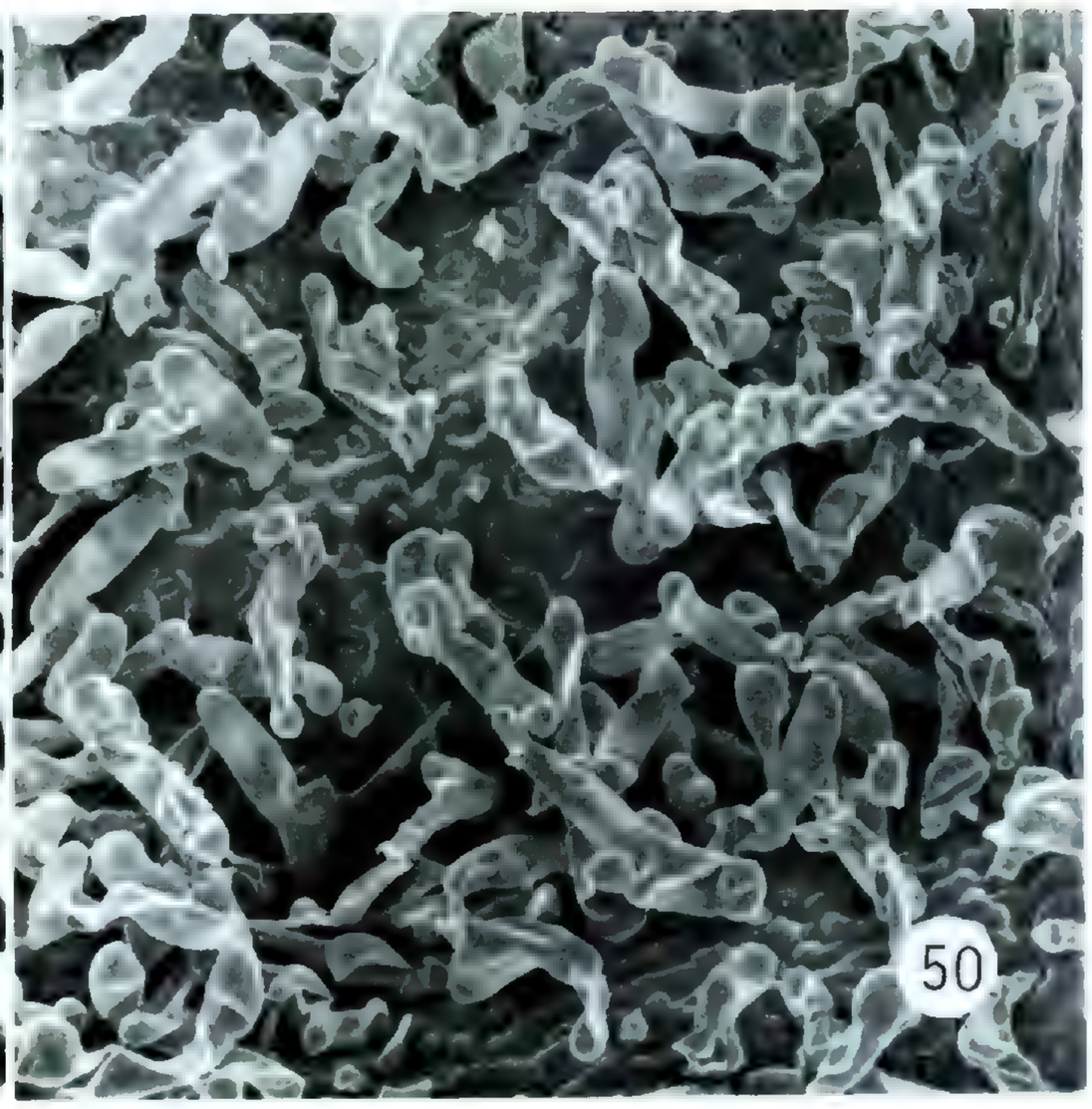
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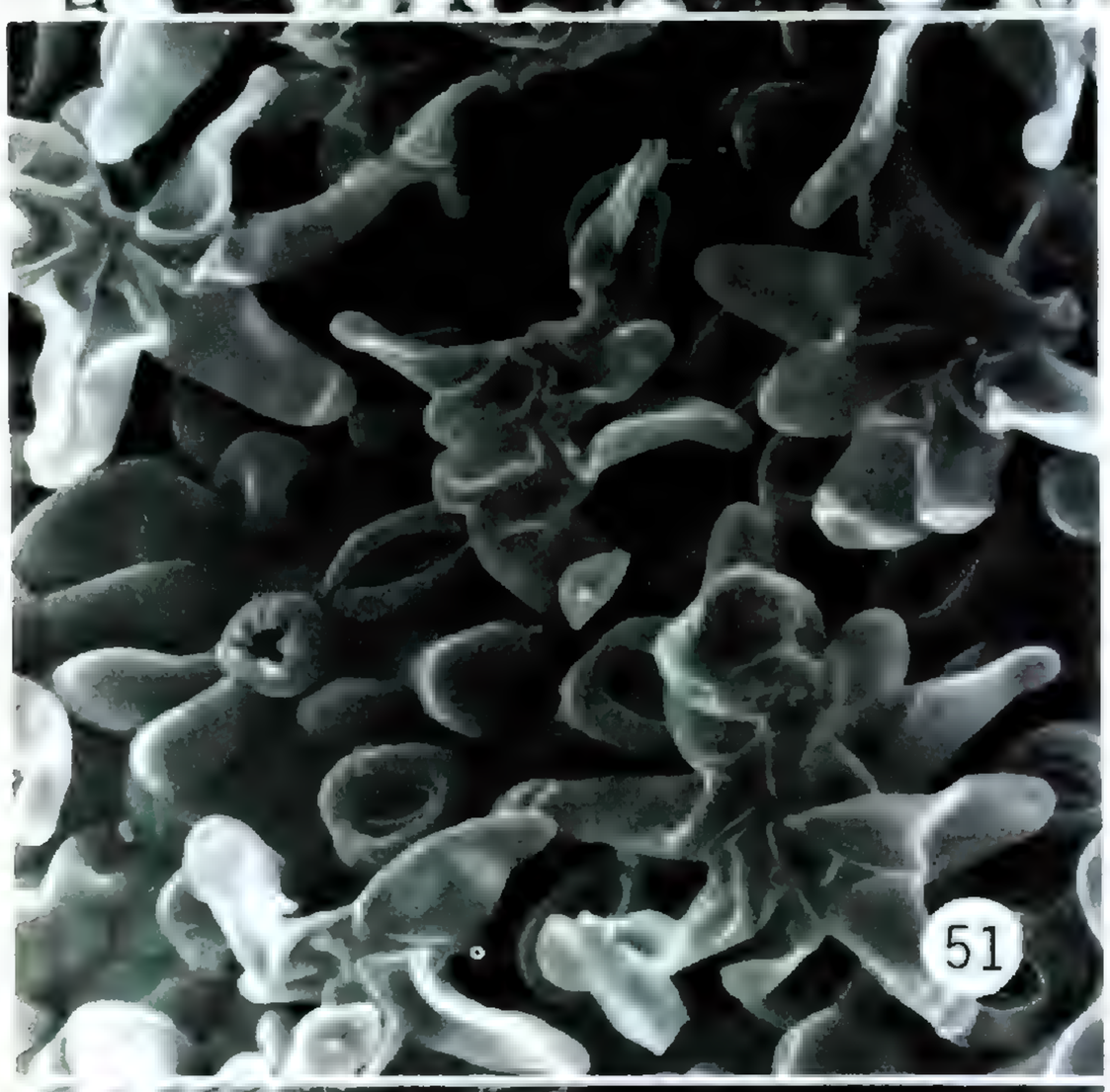
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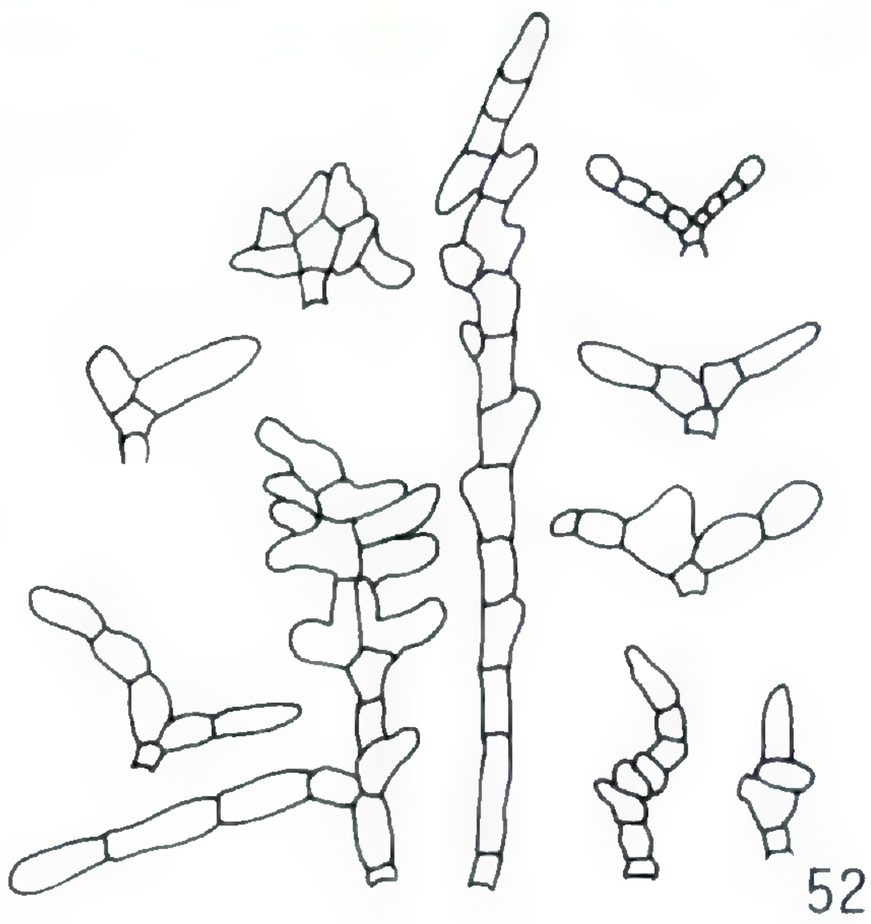
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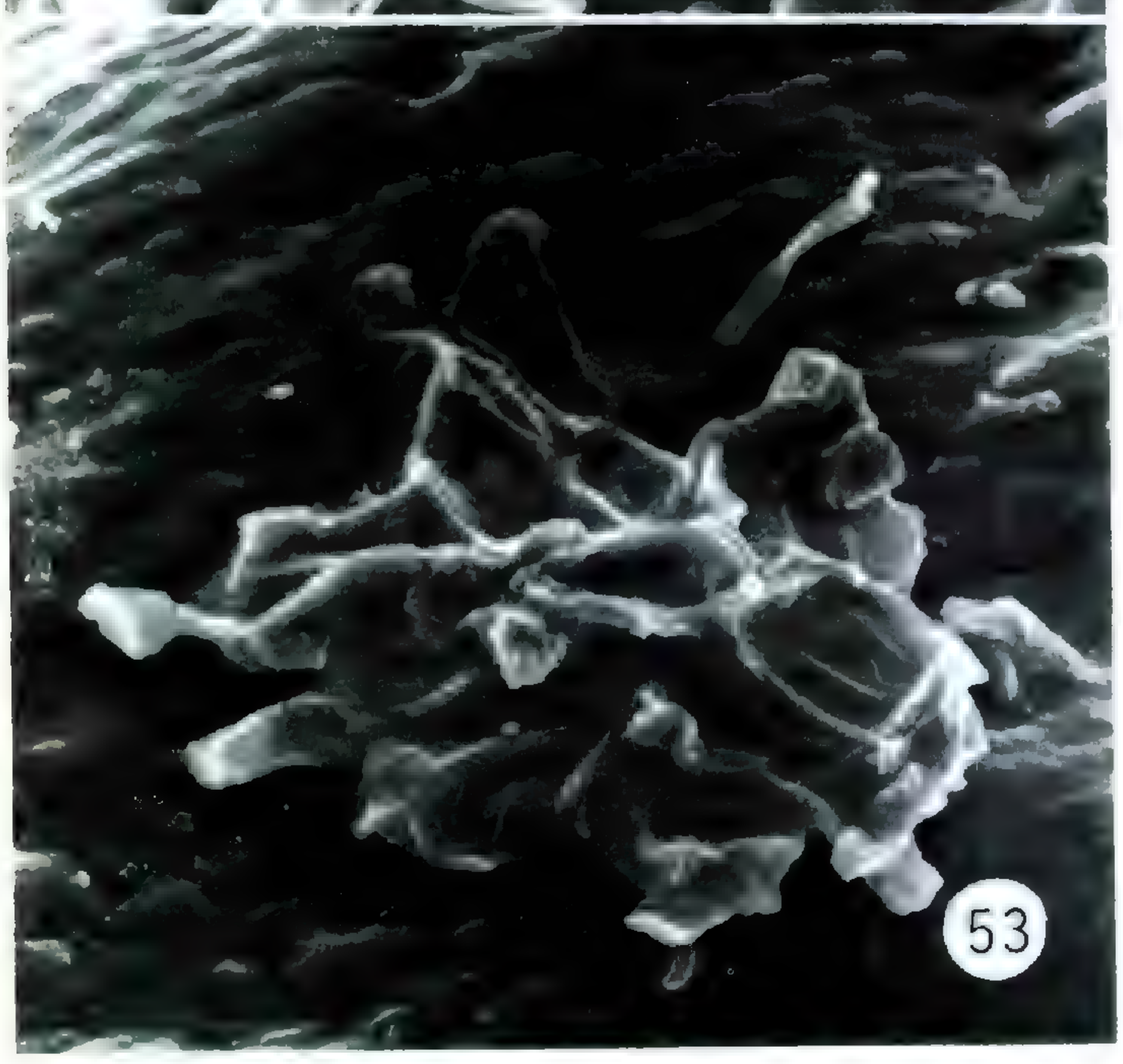
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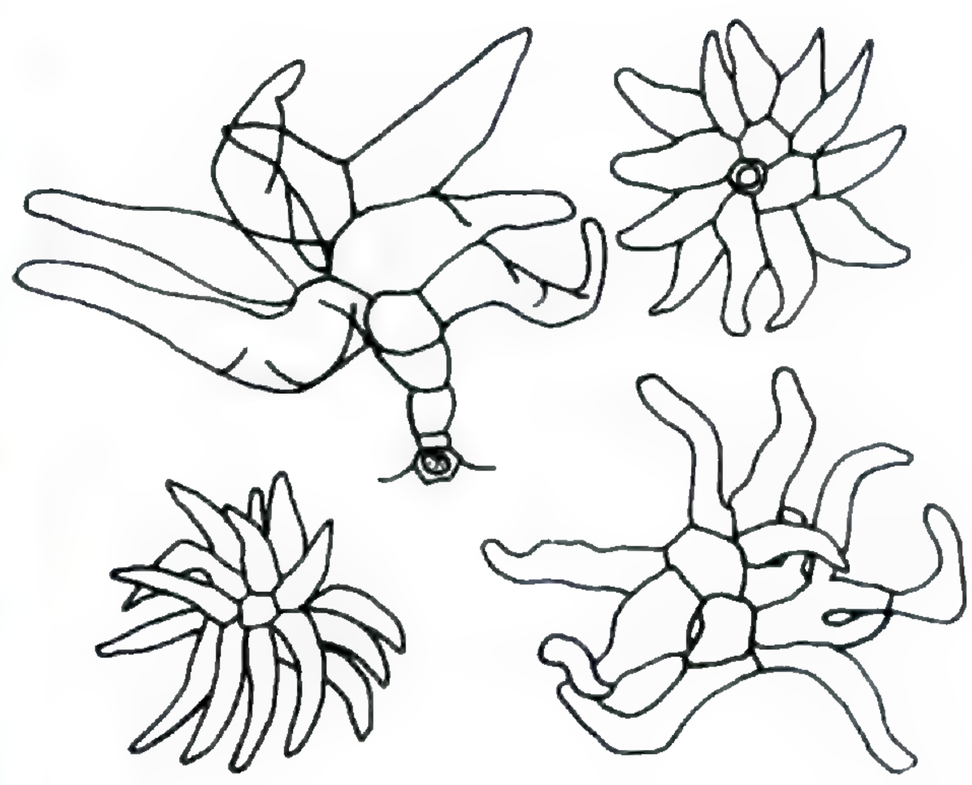
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FOSSIL EVIDENCE REGARDING THE EVOLUTION OF *NOTHOFAGUS* BLUME

EDGARDO J. ROMERO[1]

ABSTRACT

Information on fossil *Nothofagus,* and related genera, is reviewed based on pollen grains, leaves, woods, and flowers and fruits. The available data suggest that ancestors of *Nothofagus* and related families probably originated in West Gondwanaland. By the Santonian, *Nothofagus* was the only living genus already differentiated in the southern Hemisphere. Northern counterparts included several species in living genera of the Betulaceae, Myricaceae, and Ulmaceae. Rapid evolution and speciation of *Nothofagus* took place in the Eocene. After the pollen types and the main leaf forms were established in the Cretaceous and Eocene, respectively, the rate of morphological change was slow. More speciation was possible after the Miocene in New Guinea and also in other areas during the Plio-Pleistocene. Several lines of evidence support former suggestions of giving *Nothofagus* a higher taxonomic rank.

Nothofagus Blume has frequently captured the interest of botanists and paleobotanists. It plays a dominant role in the temperate forests of the Southern Hemisphere, has economic importance as a timber source, and has an intriguing distribution as a vicariant of the other genera in Fagaceae. It comprises 34 species living in South America, Australia, New Zealand, New Caledonia, and New Guinea. It certainly lived in Antarctica, but perhaps never in South Africa.

The Fagaceae are usually associated with the Betulaceae in the order Fagales (Thorne, 1983; Takhtajan, 1980), sometimes including also the Balanopaceae (Cronquist, 1968). Other related orders are Didymelales, Casuarinales, Myricales, and Hamamelidales, all included in the subclass Hamamelidae. Although this subclass has been subjected to considerable systematic rearrangement (Thorne, 1973), the taxa mentioned above were not very much affected.

The Fagaceae have been segregated into three subfamilies since De Candolle (1864), and this classification has been supported by modern studies such as those of Forman (1966) and Hjelmqvist (1948) on the female cupule. The only objection has been the proposal to segregate *Nothofagus* as a new family, made by Kuprianova (1965), on the basis of the pollen grains. More recent support for some kind of segregation was advanced by Crepet and Daghlian (1980), Smiley and Huggins (1981), Thorne (1983), Nixon (1984), and Jones (1984b). The classification of the species of *Nothofagus* into two sections and four series was suggested by van Steenis (1953) and Soepadmo (1972) on the basis of the female cupule and vegetative morphology. Recent information does not support fully such an arrangement (Elias, 1971; Philipson & Philipson, 1979; Hill, 1983), but no alternative system has been proposed.

In recent years a growing body of information has accumulated about fossil materials of *Nothofagus* and related genera, shedding some light on its history and phylogenetical development. This information has not been fully used, and speculation about the evolution and paleobiogeography of the genera has been based mainly on the evidence of living plants (van Steenis, 1971; Darlington, 1965; Melville, 1973, 1981; Cracraft, 1975; Humphries, 1981, 1985; Heads, 1985). Therefore, it seems reasonable to review information concerning fossil forms.

Modern and fossil data are reviewed first in this paper, followed by a discussion. The review of fossil data is arranged by type of fossil (pollen, leaves, woods, and flowers and fruits). In each case, a brief statement about their morphology in living plants is given. The discussion starts with the Cretaceous history of the genus, and also deals with the fossil record of related families. Then, the Paleogene account comprises the differentiation of species within the genera, so the morphology of the living ones is also considered. Finally, the Neogene part deals mainly with biogeography, and the information concerns primarily living plants. The fossil evidence was compiled by Wolfe (1973) and Muller (1981). When some information is given without men-

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tioning the source, it may be found in these reviews. However, in important cases the original publication is given. Other more recent papers, or ones not considered by Wolfe or Muller, are quoted as well. The references to paleogeography are based on Smith et al. (1981) and those to age are based on Harland et al. (1982).

Data

POLLEN GRAINS

Pollen grains of *Nothofagus* are highly characteristic and easily determined. They are small- to medium-sized, peroblate, stephanocolpate, crassimarginate, with a spinulose exine. The living species have been studied in detail by Hanks and Fairbrothers (1976) and Praglowski (1981, 1982). There are three different types ("*brassi,*" "*fusca,*" and "*menziesi*") differing in the shape of the mesocolpi, and the size and thickening of the colpi. These pollen grains are very different from others in related genera within Fagaceae, or in related families, which are mostly tricolporate, with variable, non-spinose sculpturing.

Fossil pollen grains provide the most complete record of *Nothofagus* through geological time. They appear for the first time in sediments of Santonian age in southern Australia (Dettmann & Playford, 1969; Stover & Evans, 1973) with the "*brassi*" type. This type was found also in the Campanian of New Zealand (Couper, 1960) and in the Maastrichtian of South America (Archangelsky & Romero, 1973; Romero, 1973). The "*fusca*" type was present in the Maastrichtian of New Zealand and South America and the Paleocene of Australia (Cooper, 1960; Romero, 1973; Martin, 1981). The "*menziesi*" type was recorded for the first time in the Maastrichtian of South America, and then in the Paleocene of New Zealand and the Eocene of Australia (Cooper, 1960; Romero, 1973; Martin, 1981). Since their first appearance in the Cretaceous the three types of pollen grains show almost no morphological change.

During the Eocene and Oligocene the participation of *Nothofagus* in pollen assemblages reached its maximum (Romero, 1973, 1977; Martin, 1982). During the Miocene it was generally less frequent but it expanded its area, and is recorded for the first time in New Guinea ("*brassi*" type; Khan, 1974). There are no records of fossil *Nothofagus* from New Caledonia.

Pollen grains of genera related to *Nothofagus* are also present relatively early. "*Celtis* type" pollen and "intermediates to *Ulmus* type," as defined by Muller (1981) were described from the Turonian (ca. 90 Ma) of Borneo. Borneo was located close to or at the Equator at that time. Pollen grains of *Alnus, Betula,* and *Myrica* were found in the Santonian of Japan, Canada, and the United States, respectively (see Muller, 1981 for references in this paragraph). In the Campanian *Cercidiphyllites* is recorded in Canada, *Momipites* (Juglandaceae) in the United States, and *Castanea* in Canada and Holland. The last one is the first genus of Fagaceae recorded in Laurasia, about 15 Ma, later than the occurrence of *Nothofagus* in Gondwanaland. In the Maastrichtian, the "*Ulmus* type" was described in Canada, the United States, Brazil, and India. In the Paleocene the "*Liquidambar* type" (Hamamelidaceae), *Tricolporopollenites parmularius* (Eucommiaceae), and *Carpinuspollenites* (Betulaceae) are all known from central Europe. More importantly two other families of the subclass Hamamelidae with a Gondwanaland distribution appear for the first time during the Paleocene. They are Casuarinaceae, represented by *Haloragacidites* in the Paleocene of New Zealand, Australia, Argentina, and sediments in the Indian Ocean, and Didymelaceae, represented by *Schizocolpus marlinensis* in New Zealand and sediments of the Indian Ocean.

LEAVES

Leaves of living species of *Nothofagus* are rather variable. Those of extant South American, Australian, and New Zealand species (Romero, 1980; Carrasco Aguirre & Romero, 1982) are persistent or deciduous, craspedrodomous (with one exception), and with well marked, sometimes composite teeth. Those of New Guinea and New Caledonia (Romero & Carrasco Aguirre, 1982) are persistent, brochidodromous or semi-craspedrodomous, entire margined or with small teeth. The small teeth are different from those in the former species and were probably independently derived. Leaves of living species of *Fagus* can be differentiated from *Nothofagus* (Jones, 1984a; Dibbern & Romero, 1984; Romero & Dibbern, 1985) and the same is true for other genera of Fagaceae and related families (Wolfe, 1973). Cuticles of the South American species were studied by Ragonese (1981) while Jones (1984a) also sampled several species from Aus-

tralia, New Zealand, New Guinea, and New Caledonia.

Imprints of leaves of indubitable *Nothofagus* fossil species are not present until the Eocene, and they are probably more frequent during the Oligocene (Ettingshausen, 1886, 1888; Dusen, 1907, 1916; Romero, 1978; Holden, 1983; Hill, 1983). Several show strong similarities with living species, and thus indicate a very low rate of morphological change (Dibbern & Romero, 1984).

Species of *Ulmus, Betula,* and *Alnus* were also described in the Southern Hemisphere (Ettingshausen, 1886, 1888; Dusen, 1907, 1916) and they will probably prove to be *Nothofagus*. However, it is noteworthy that a revision (Romero & Dibbern, 1985) of the original types of Dusen showed that some South American fossils described as *Fagus* could not be classified among living *Nothofagus* and fall within the limits of variation of *Fagus*.

Upper Cretaceous and Paleogene sediments both in the Gondwanaland and Laurasian continents also yielded some extinct genera of supposed Fagaceae, such as *Debeya, Dryophyllum, Fagophyllum,* and *Fagopsis* (Ettingshausen, 1886, 1888; Dusen, 1916; Berry, 1937). However, the delimitation and definition of these genera was done also many years ago in the Northern Hemisphere, and was based only on gross morphology. Its use, especially in Gondwanaland, should be revised in the light of modern concepts of leaf architecture. The studies of Manchester and Crane (1983) and Jones (1984a) show the trend to be followed.

Among related families, important records of fossil leaves are those of *Alnus* from the Maastrichtian of British Columbia; *Corylopsis, Corylus,* and *Sinowilsonia* from the Paleocene; and *Carya* and *Tetracentron* from the Eocene, from several localities in the United States (see references in Wolfe, 1973).

Without familial or ordinal assignment, the earliest fossil leaves considered "to be members of a trend" to the subclass Hamamelidiae are some "Platanoids" from the Albian of the Potomac Group, eastern United States (Hickey & Doyle, 1977; Doyle & Hickey, 1976). Another early leaf that shared some Hamamelidoid and Magnolioid characters is an unnamed one, from the Baqueró Formation in Patagonia, Argentina and is late Barremian to early Aptian in age (Romero & Archangelsky, 1985).

Cuticles of fossil *Nothofagus* have been studied in a few Eocene and Oligocene species by Hill (1983) and Jones (1984a).

WOODS

Nothofagus timber has commercial value and its anatomy has been well known for many years (Dadswell & Eckersley, 1935; Dadswell & Ingle, 1954; Hinds & Reid, 1957; Tortorelli, 1956; Wagemann, 1948). Practical keys for use in each country were published, allowing identification of every species.

Fossil woods of *Nothofagus* have been described from strata of different ages in South America. The oldest is *Nothofagoxylon pichasquensis* (Torres & Rallo, 1981) from the Upper Cretaceous of northern Chile. It is associated with dinosaurs and turtles, at about 25°S of paleolatitude. Seven other species were found in Eocene, Oligocene, or undifferentiated Tertiary rocks (see review in Ragonese, 1977; and Torres, 1984). In Oligocene (?) sediments of Río Turbio, southernmost Argentina, Salard (1961) described a species of *Fagoxylon*.

A doubtful *Nothofagoxylon* was studied from New Zealand (Evans, 1931). As far as I am aware, there are no other woods described as *Nothofagus* in recent times. Among related families, there is an important record of woods of Platanaceae in the Campanian of the United States, which is the first record of woods of the subclass (Wolfe, 1973).

FLOWERS AND FRUITS

The cupule of *Nothofagus* is interpreted as a reduced dichasium (Forman, 1966). Its relationships with other genera have been established by Forman (1966) and Endress (1977). One of the species (*N. alessandri*) has retained seven flowers, which is probably the most primitive number of flowers in the family. *Nothofagus nitida* occasionally has five (van Steenis 1953: 312).

The only flower reported from the Southern Hemisphere is a four-parted cupule from the Oligocene of Tasmania (Hill, 1983) whose affinities to living species could not be established. In the Northern Hemisphere several flowers were attributed to Fagaceae and related families (Crepet, 1981; Smiley & Huggins, 1981). *Fagopsis,* from Eocene and Oligocene beds in the United States, is especially important (Manchester & Crane, 1983). It is a representative of the Fagaceae, but it is not readily accommodated in any recent subfamily. It has some features similar to every genus in the family, except *Nothofagus*.

Discussion: A Phylogenetic and Paleogeographical Model

On the basis of the preceding data, a scenario may be constructed for the history of *Nothofagus* and related taxa through geological time. The current paradigm for the origin of the angiosperms is that they derived from unknown gymnosperms some place in West Gondwanaland towards the end of the Early Cretaceous (Raven & Axelrod, 1974; Brenner, 1976; Doyle & Hickey, 1976; Schuster, 1976). The subclass Hamamelidae would differentiate in the Northern Hemisphere. Raven and Axelrod (1974) stated that families like Hamamelidaceae, Fagaceae, and Betulaceae would have originated in Laurasia, and particularly *Nothofagus* migrated from Asia through Gondwanaland, via the mountain heights of Africa and India, in the Middle Cretaceous. Wolfe (1973) also believed that most of the Hamamelidae originated in the *Aquilapollenites* province (western North America and Asia) in the Late Cretaceous, and that families such as Fagaceae and Betulaceae evolved there prior to the Maastrichtian, diversifying into extant genera during the Maastrichtian and Paleocene.

The fossil record does not fully support these ideas. As mentioned in the previous chapter, there are leaves of Aptian–Albian age with Hamamelidoid features in relatively high latitudes of both hemispheres. The oldest fossil record determined to family are pollen grains of Ulmaceae of Turonian age in the equatorial belt, in Borneo. And the oldest determined to genus are pollen grains of Santonian age, also at high latitudes in both hemispheres: *Nothofagus* in Australia and *Alnus, Betula,* and *Myrica* in Japan, Canada, and the United States. Therefore, it seems more plausible that the subclass originated in tropical areas of West Gondwanaland, with different families differentiating polewards. *Nothofagus* was at that time the only representative of Fagaceae being a vicariant of the northern Betulaceae and Myricaceae. Such an early differentiation of only this genus from related families would support the above mentioned suggestion to segregate Nothofagaceae as an independent family.

From West Gondwanaland, the ancestors of *Nothofagus* should have migrated to southern South America and/or southern Africa. South America was at that time united to west Antarctica, which in turn was very close to or at the South Pole. Southern Africa was separated from east Antarctica, but only by about 1,000 km; the coast of east Antarctica was probably at about 60°S. From west or east Antarctica the ancestors of *Nothofagus* should have reached Australia before the Santonian and New Zealand before the Campanian.

Campanian and Maastrichtian times witnessed the diversification and migration of *Nothofagus,* which occupies every Gondwanaland land mass, except South Africa and India, and is recorded with the three types of pollen grains and petrified trunks. In the Laurasian continents, in contrast, there is a radiation of different families: Platanaceae, Cercidiphyllaceae, Juglandaceae, and Fagaceae (Castaneoideae), which may be found in widespread outcrops as different kinds of fossils.

By the Paleocene and Early Eocene, *Nothofagus* was represented in the Southern Hemisphere, though it was still not dominant. Casuarinaceae and Didymelaceae, the two other southern families of the subclass, are recorded for the first time. Also there are some cosmopolitan genera (*Dryophyllum, Fagophyllum*) usually, yet with growing hesitation, attributed to the Fagaceae. In any event, there is evidence for a relatively important hamamelidaceous genetic stock in the Southern Hemisphere. In the Northern Hemisphere the radiation continued, with records of the new families Eucommiaceae and Hamamelidaceae, and more genera in the Platanaceae, Betulaceae, Ulmaceae, and Juglandaceae. The Fagaceae were still only represented by the Castaneoideae.

During the Eocene the Fagaceae had a rich fossil record comprised of every kind of fossil. In South America, *Nothofagus* is represented by abundant woods, leaf imprints, and pollen grains, and may be dominant in the floras. Australian authors (Christophel, 1981; Martin, 1981, 1982) remarked that in Australia pollen grains of *Nothofagus* may be very abundant in Eocene sediments, but imprints of leaves are very rare, if even present. This is explained by a mosaic pattern of forests with patches of a subordinate *Nothofagus,* but with favorable conditions for dispersal of the pollen grains.

Fagaceous leaves of Eocene deposits are the oldest that can be placed in extinct species of living genera. They belong to *Quercus,* "*Castanea,*" and *Fagus* in the Northern Hemisphere and to *Nothofagus* in the Southern Hemisphere.

As noticed above, very low rates of morphological change in *Nothofagus* are recorded in their pollen grains since the Cretaceous and in their

leaves since the Eocene. These long periods of stasis seem to conform to the "punctuated equilibrium" model of evolution. However, the process and timing of the radiation of the stable species in both cases is not well established.

Most of the South American fossil leaves that resemble those of living species are similar to the deciduous taxa inhabiting the northern part of *Nothofagus* distribution, in northwest Patagonia (Romero & Dibbern, 1985). Also I restudied fossil leaves from Australia, formerly published by Ettingshausen (1888) and found that deciduous species were present there at the same time. Therefore, there is a strong possibility that we are witnessing in these floras the development of deciduousness in *Nothofagus,* or at least an adaptive radiation from deciduous ancestors in Antarctica. About 35 to 40 Ma, that is, by Late Eocene or Early Oligocene, Australia was separated from Antarctica (Raven & Axelrod, 1972; Kemp, 1978). A more continuous oceanic current developed around Antarctica, substantially changing the climate of the Southern Hemisphere. The development of deciduousness was a probable response to that change (Romero, 1984). Later, in connection with the migration of Australasia to the north (Kemp, 1978; Martin, 1981; Smith et al., 1981), some extinction occurred there leaving the Tasmanian *N. gunni* as the only deciduous species.

Leaf taphofloras and palynofloras of Eocene and Oligocene age show repeatedly a mixture of species of supposed cold temperate climate with others of supposed subtropical or tropical climate (Kemp, 1978; Romero, 1978, 1984). They are rather variable through geological time and latitude, and have different percentages of *Nothofagus* as the most important cold temperate element. The same authors suggested that these Paleogene associations are not represented by any of the living plant associations.

A problem is imposed by the presence in South America of fossils attributed to Fagaceae, which are beyond the range of variation of *Nothofagus* and within that of *Fagus.* They are leaves and woods and were reported as southern *Fagus.* Similar but more doubtful remains were described from Australia and New Zealand. A genetical relationship with *Fagus* seems unlikely, and it is more reasonable to expect some kind of convergence between taxa belonging to the same genetic stock (no matter if it is considered at the familial, ordinal, or superordinal level) and that have remained isolated since the Cretaceous. A similar and consistent case for convergence could also be made for supposed *Nothofagus* widespread in North America (Elsik, 1974). They are not really *Nothofagus* (Romero, 1977: 181; Muller, 1981) but share important characters.

The oldest records of pollen grains of *Quercus* and *Fagus* are from the Oligocene, several million years after the first record of leaves (Romero, 1984). This contrasts with the long history of the pollen grains of *Nothofagus* and supports the consideration of the southern genus as a more independent, earlier derived taxon. Also, the Oligocene record of *Fagopsis* in the United States, showing features of different genera of Fagaceae, except *Nothofagus,* is additional argument for an independent treatment of this genus.

During Late Eocene and Oligocene times, New Guinea rose above sea level (Axelrod & Raven, 1982). The earlier records of *Nothofagus* are pollen grains of Miocene age. Raven and Axelrod (1972) suggested that the genus migrated from northwest Australia and then diversified during the Pleistocene. New Caledonia has remained isolated since the Cretaceous, and has no fossil record. Raven and Axelrod (1972) believed that the *Nothofagus* species also remained isolated and are remnants of the old Antarctic stock. Therefore, according to these authors, New Guinea and New Caledonia received different contingents of species, from different continents and with a gap of about 50 million years. However, the living plants in both archipelagos are extremely similar in their flowers (Soepadmo, 1972), leaves (Romero & Carrasco Aguirre, 1982), pollen grains (Cookson & Pike, 1955), wood (Dadswell & Ingle, 1954), and ecology (Ash, 1982). The botanical evidence seems to indicate that the migration occurred from one of the archipelagos to the other, but it is not clear which one was the source and when it happened.

The Pliocene and Pleistocene were times of important climatic changes, related to glaciation and fluctuations of sea level. They produced extinctions in some groups of plants and diversification in others. Extinctions occurred with the species producing pollen of the "*brassi*" type in South America, New Zealand, and Australia. Radiation occurred in New Guinea, where the uplift of the mountains favored the differentiation of 13 still closely related species.

There are also other groups of species very similar morphologically, which probably differentiated very recently. One group is that of *N.*

betuloides, N. dombeyi, and *N. nitida,* with similar flowers (van Steenis, 1953), leaves (Romero, 1980), cuticles (Ragonese, 1981), and pollen (Heusser, 1971; Markgraf & D'Antoni, 1978), which may produce hybrids in mixed populations (Donoso & Atienza, 1984). Another group of this kind, in New Zealand, is that formed by *N. fusca* and *N. truncata,* which have the same similarities and frequently hybridize (Cockayne & Atkinson, 1926). Finally, *N. antarctica* has marked ecotypes, and *N. solandri* has subspecies, which are evidences of very recent pressure of selection towards speciation.

Conclusions

The fossil record supports several plausible hypotheses regarding the evolution of *Nothofagus* and related taxa. They are:

1) Ancestors of Hamamelidales and related orders differentiated in tropical areas, in West Gondwanaland. By the Santonian they had migrated toward Laurasia, where Ulmaceae, Betulaceae, and Myricaceae radiated, and towards southern Gondwanaland, where only *Nothofagus* ancestors evolved. This would support the suggestion of giving a higher rank to the southern genus.

2) *Nothofagus* ancestors migrated from tropical West Gondwanaland to southern South America–west Antarctica, and/or to southern Africa–east Antarctica. From Antarctica they reached Australia in the Santonian and New Zealand in the Campanian.

3) During the Eocene living genera of Fagaceae differentiated in the Northern Hemisphere and direct ancestors of living species of *Nothofagus* differentiated in the Southern Hemisphere. These changes are registered by fossil leaves that represent the onset of deciduousness in response to global climatic changes. Deciduous species of *Nothofagus* were present in Australia and New Zealand, but were subsequently lost.

4) Long periods of stasis in the morphological change of fossil species seem consistent with the punctuated equilibrium model, but the early, rapid differentiation of the group is not yet well documented.

5) During Eocene times, *Nothofagus* was a member of mixed forests, comprised of subtropical and temperate elements.

6) *Nothofagus* reached New Guinea by Oligocene or Miocene times. The circumstances of migration to New Caledonia are not clear. Botanical evidence is consistent with exchanges between the two archipelagos.

7) Climatic changes during the Pliocene and Pleistocene were responsible for the extinction of the *Nothofagus* "*brassi*" group in Australia, New Zealand, and South America, as well as for speciation between several closely related modern species.

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EVOLUTION AND REPRODUCTIVE BIOLOGY OF INFLORESCENCES IN *LITHOCARPUS, CASTANOPSIS, CASTANEA,* AND *QUERCUS* (FAGACEAE)[1]

ROBERT B. KAUL[2]

ABSTRACT

Of *Lithocarpus, Castanopsis, Castanea,* and *Quercus* only *Lithocarpus* frequently bears branched spikes suggestive of the primitive condition in the Fagaceae; the other genera sometimes have them in some individuals. Simple and branched spikes can occur on the same tree. Evolution of the simple spike is interpreted as the loss of branching capacity in the branched spikes. The Fagaceae show various transitional stages from perfect, entomophilous to imperfect, anemophilous flowers and from mixed-sex to unisexual spikes. Complete separation of staminate from pistillate function into separate spikes and catkins occurs only in *Quercus,* which is also the only anemophilous member of these four genera. *Lithocarpus* is the least specialized while *Quercus* is the most specialized in inflorescence structure of the four genera.

Pathways of inflorescence evolution in *Castanea, Castanopsis, Lithocarpus,* and *Quercus* have been proposed that identify *Lithocarpus* and *Quercus* as possessing the least and most specialized inflorescences, respectively (Kaul & Abbe, 1984). The specialized inflorescence character states of *Quercus* are associated with anemophily and the less specialized states in *Lithocarpus, Castanea,* and *Castanopsis* relate to their entomophily (Kaul, 1985). Kaul et al. (1986) suggested that the evolution of anemophily in *Quercus* [and probably also in another fagaceous species, *Trigonobalanus daichangensis* (Camus) Forman] was an adaptation for successful pollination in seasons of low pollinator activity in seasonal climates, for example, spring in the temperate latitudes. In such latitudes the anemophilous Fagaceae—*Quercus* and *Fagus*—flower briefly in the spring whereas the entomophilous *Castanea* and northerly species of *Castanopsis* and *Lithocarpus* flower over a longer period in early summer. Likewise, flowering peaks in entomophilous paleotropical Fagaceae (*Castanopsis, Lithocarpus*) coincide with maximum insect activity (Kaul et al., 1986; cf. Fogden, 1972). *Quercus,* which is anemophilous throughout its range, flowers at various times in the tropics but not in the wettest seasons. Further evidence of the functional aspects of these inflorescences is scanty, and therefore definitive answers to questions about the ancestry and subsequent functional evolution of fagaceous inflorescences must be sought through comparative studies of living and fossil taxa.

In these genera the spikes and catkins usually bear numerous sessile, subsessile, or, in a few instances, pedunculate flower clusters that are variously called dichasia, cymules, or partial inflorescences. They are the only structures that presumably terminate in a flower in these four genera; all other structures—branches, rachises, spikes, and catkins—apparently terminate in a vegetative bud that may or may not be capable of further growth.

The dichasia are surely derived by phylogenetic condensation and the ancestral inflorescences were probably thyrse-like or panicle-like. Some modern Fagaceae, most notably some species of *Lithocarpus,* produce branched spikes that are themselves aggregated into many-branched inflorescences of higher orders, resulting in the most complex floral displays in the family.

The ancestral fagaceous inflorescence was no doubt more complex than any modern inflorescence in the family. Fey and Endress (1983) have advanced credible evidence that the cupule of the fruit is itself a product of condensation of dichasial branching systems. Further, Hjelmqvist (1948) interpreted some staminate flowers as pseudanthia. Kaul and Abbe (1984) suggested evolutionary changes in fagaceous inflorescences that included loss of syllepsis in both vegetative and reproductive shoots and separation of sta-

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ANN. MISSOURI BOT. GARD. 73: 284–296. 1986.

minate from pistillate flowers in the total inflorescence. We also suggested that the catkins of anemophilous Fagaceae were derived from spikes of entomophilous ancestors and that there is a rough gradient of decreasing inflorescence complexity with increasing latitude.

In our previous papers (Kaul & Abbe, 1984; Kaul, 1985) some complex fagaceous inflorescences were described and illustrated. Here I elaborate upon our work, illustrate additional examples of complex inflorescences, and provide further evidence for their interpretation as the least specialized forms among extant Fagaceae. It must be emphasized that even the least specialized extant forms are advanced for angiosperms as a whole, as evidenced by the presence of such extreme reductions as dichasia and cupules in every species.

Materials

I have examined thousands of specimens of paleotropical, eastern Asiatic, and North American species of *Castanea, Castanopsis, Lithocarpus,* and *Quercus* that were gathered by my colleagues and me with this and related studies in mind. All the specimens illustrated here are in my personal collection but various sets of duplicates are deposited at A, GH, K, L, and US.

Nomenclature herein follows Soepadmo (1972) for the paleotropical species and for generic delimitation.

Figures 4–16 show actual specimens portrayed diagrammatically and are not intended necessarily to be typical of the species. Blackened circles indicate pistillate dichasia and open circles indicate staminate dichasia; quantities of each are only approximated.

Terminology

Figures 1–3 illustrate many of the structures and terms used here. A *shoot system* (a major indeterminate axis with a leader that periodically undergoes extension growth, and bearing branches) can include *proleptic* or *sylleptic* shoots (produced with or without a resting period of the parent bud, respectively) or both, all or nearly all of them floriferous. Most shoots are *long-shoots* (with normally-extended internodes) but some, especially in *Quercus,* are *short-shoots* (with reduced internodes). The *total inflorescence* includes all the floriferous shoots on a shoot system. *Spikes* are non-pendent and non-foliose; they may be *simple spikes* without obvious branches or *branched spikes* that bear one or more floriferous branches. Catkins are the unbranched, pendent, staminate axes of *Quercus* and *Trigonobalanus daichangensis.* For simplicity, *bract* is used here for any non-foliar leaf homologue irrespective of its size or placement.

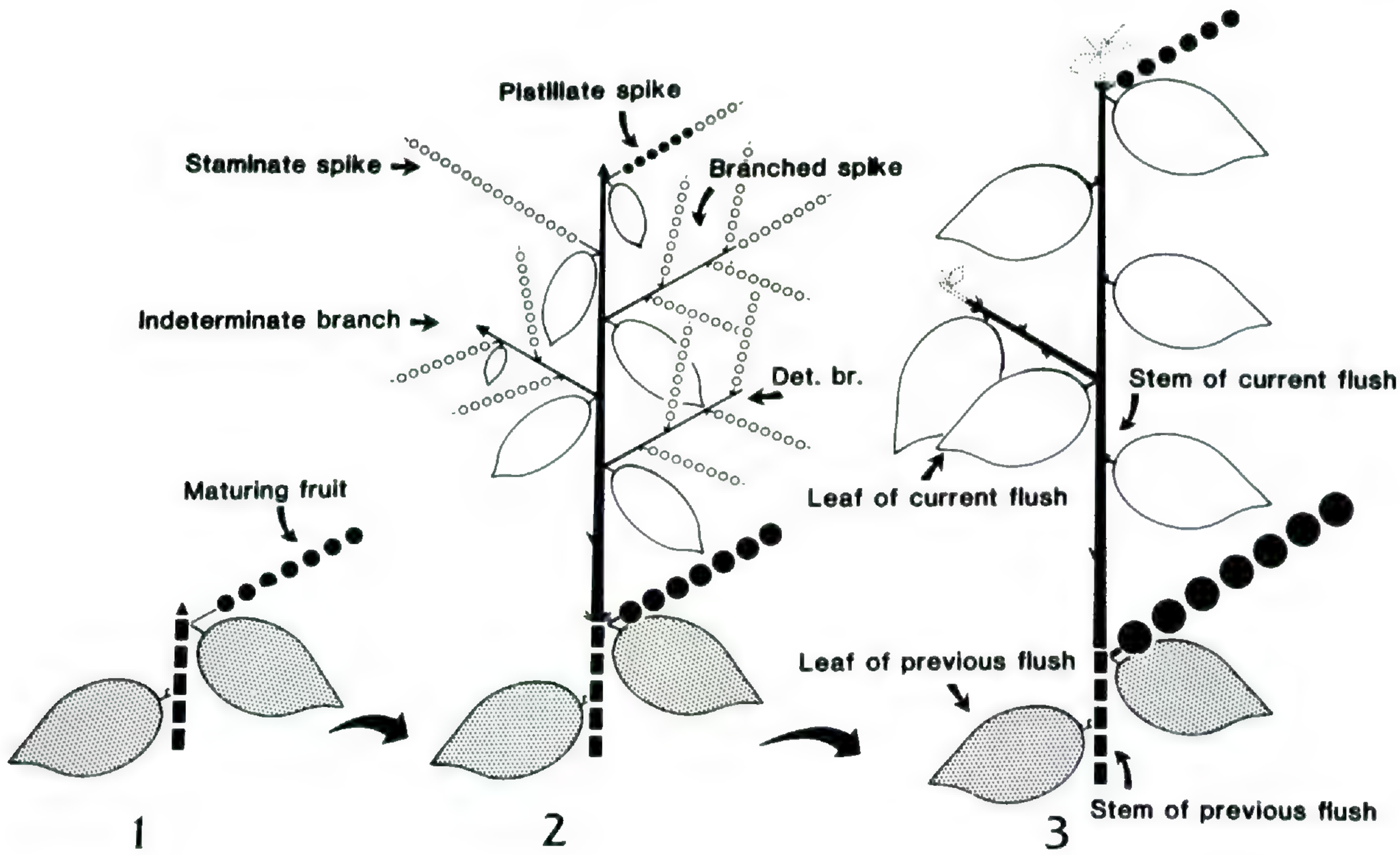
Except for the *dichasia* (a term used here generally for the flower clusters, whether or not they are strictly dichasial), all axes terminate in a vegetative bud that is often abortive. Some of these axes are capable of further growth (*indeterminate*) but some are not (*determinate*). These genera are *pantotonic* (cf. Briggs & Johnson, 1979) in that nearly every leaf- or bract-bearing node is floriferous, although not necessarily synchronously in a flush.

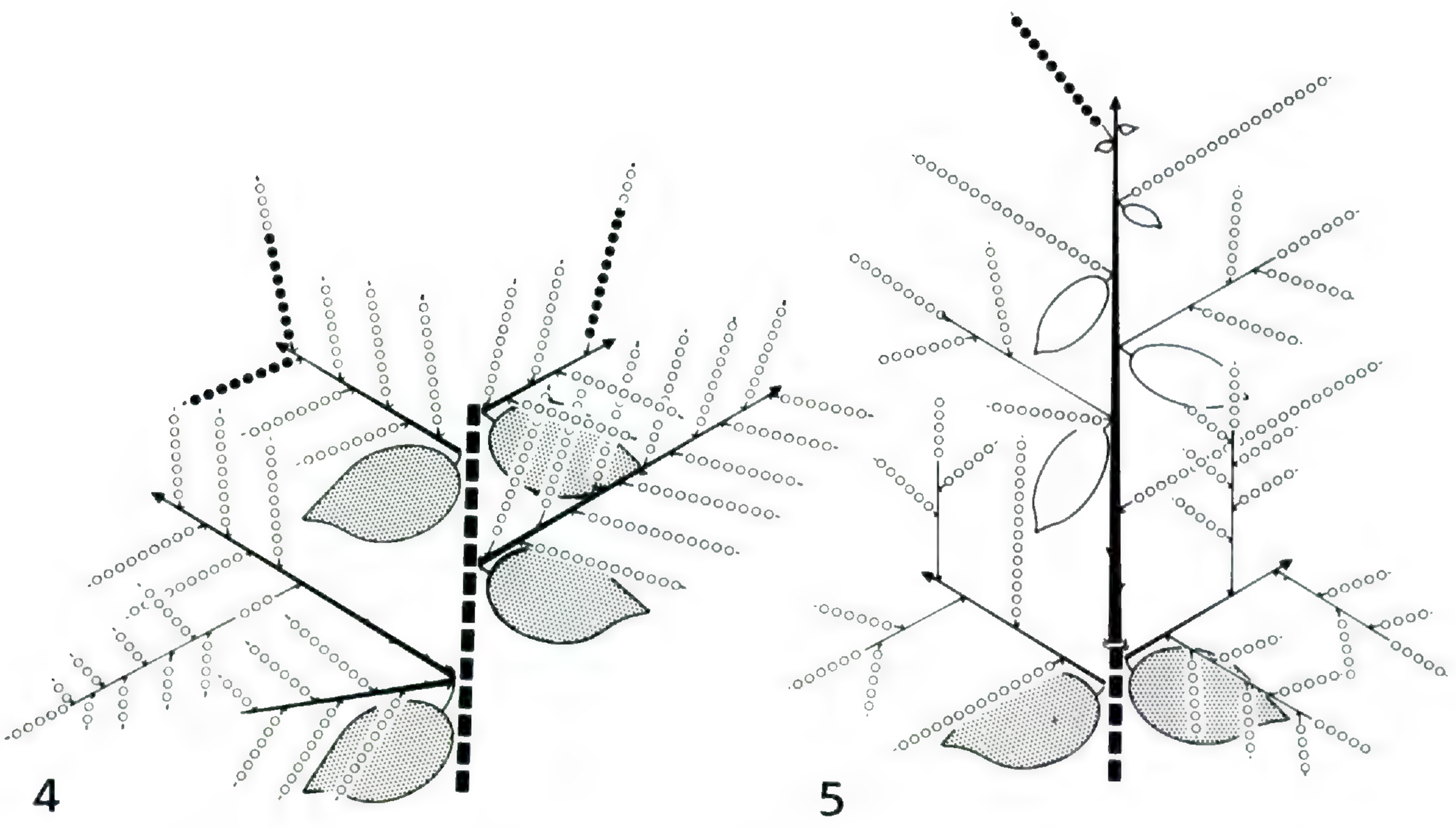
Observations

Phenology and growth habits

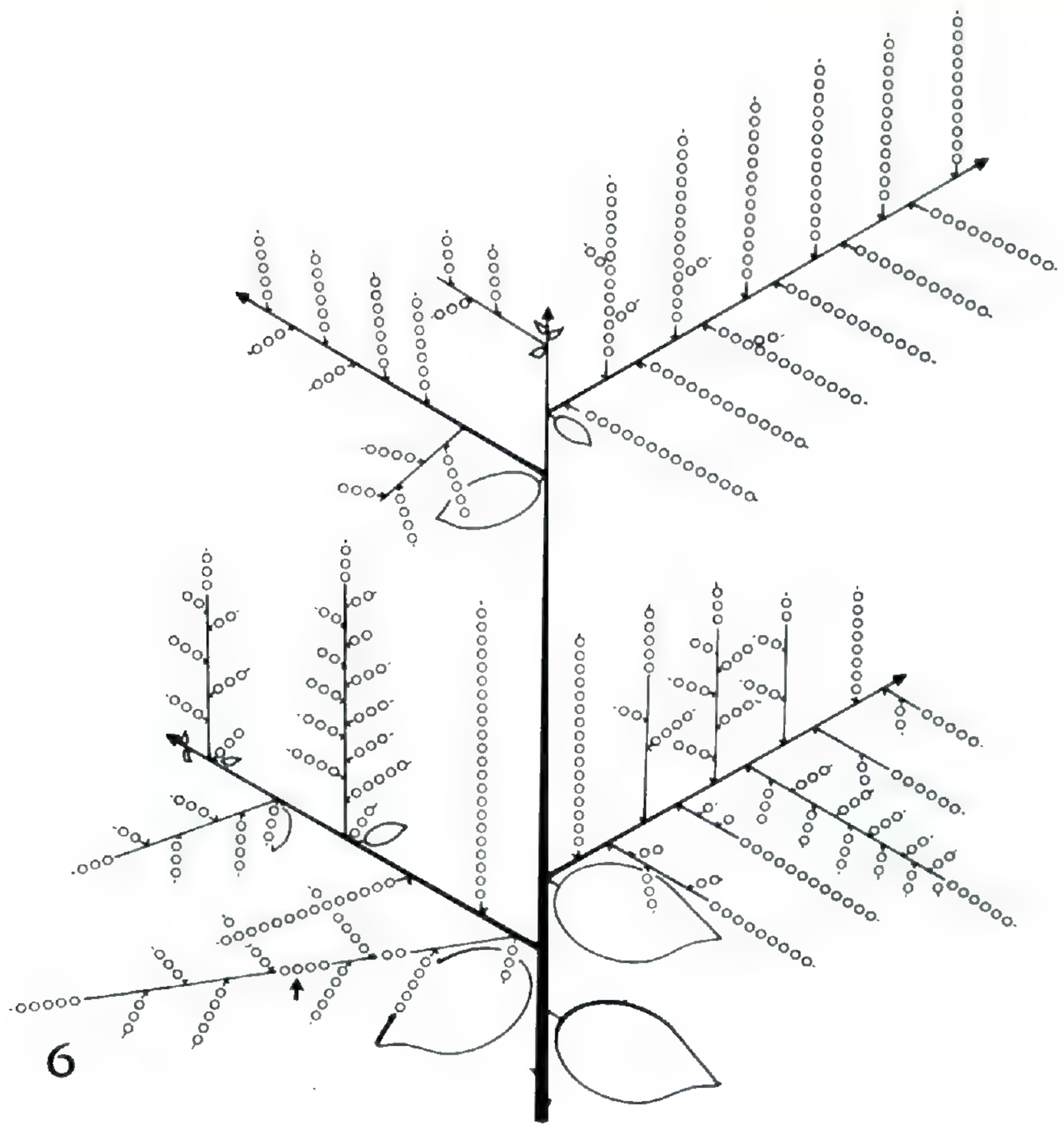
The temperate and tropical species of these genera exhibit rhythmic growth, that is, they flush at intervals. More northerly species flush more or less synchronously at a locality at least once a year in spring or early summer; some have succeeding flushes in the same growing season but only the first flush bears flowers and all but the final flush produce branches. Paleotropical species of low and middle elevations often flush and flower repeatedly in a year but there is wide intra- and interspecific variation in local flushing patterns. Sometimes the flushes are so closely spaced that anthesis in one is finishing when the next flowering begins. In some tropical lowland species flushing is non-synchronous even on a single tree (Kaul et al., 1986).

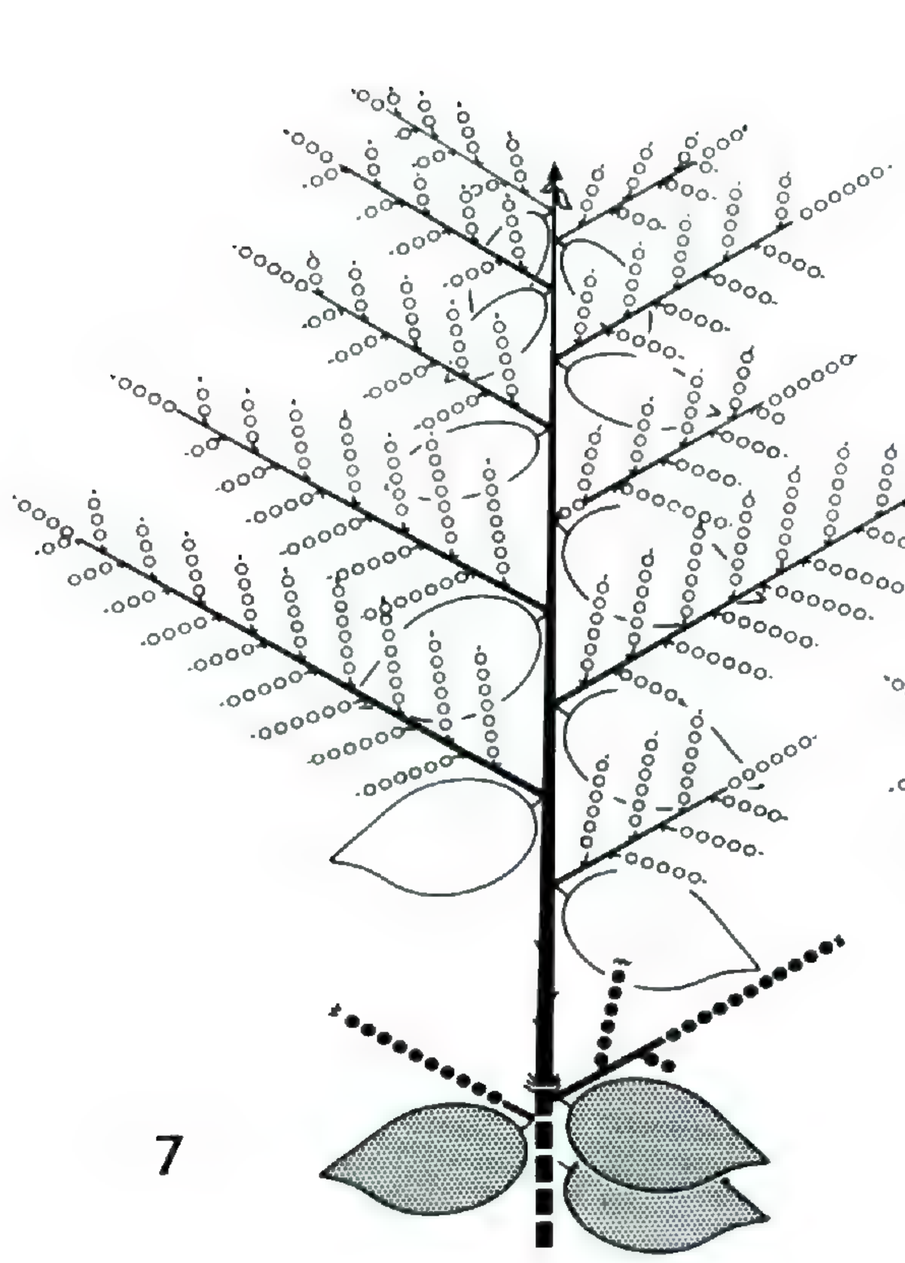
Certain principles apply to the sequence of events in the growth of the trees and some of these are illustrated in Figures 1–3. All species produce flowers on spikes or catkins borne singly or on reproductive shoots and short-shoots in the leaf axils of the current flush and often also in the axils of the previous flush. Most leaves and some bracts subtend one of these structures. In species that branch sylleptically (some species of tropical *Castanopsis, Lithocarpus,* and *Quercus*) the indeterminate shoots are also floriferous (Fig. 6 and cf. Kaul & Abbe, 1984). Fertile proleptic shoots are produced synchronously with the extension growth of the leader in a branch system (Figs. 5, 15, and numerous figures in Kaul & Abbe, 1984) but sometimes they precede it

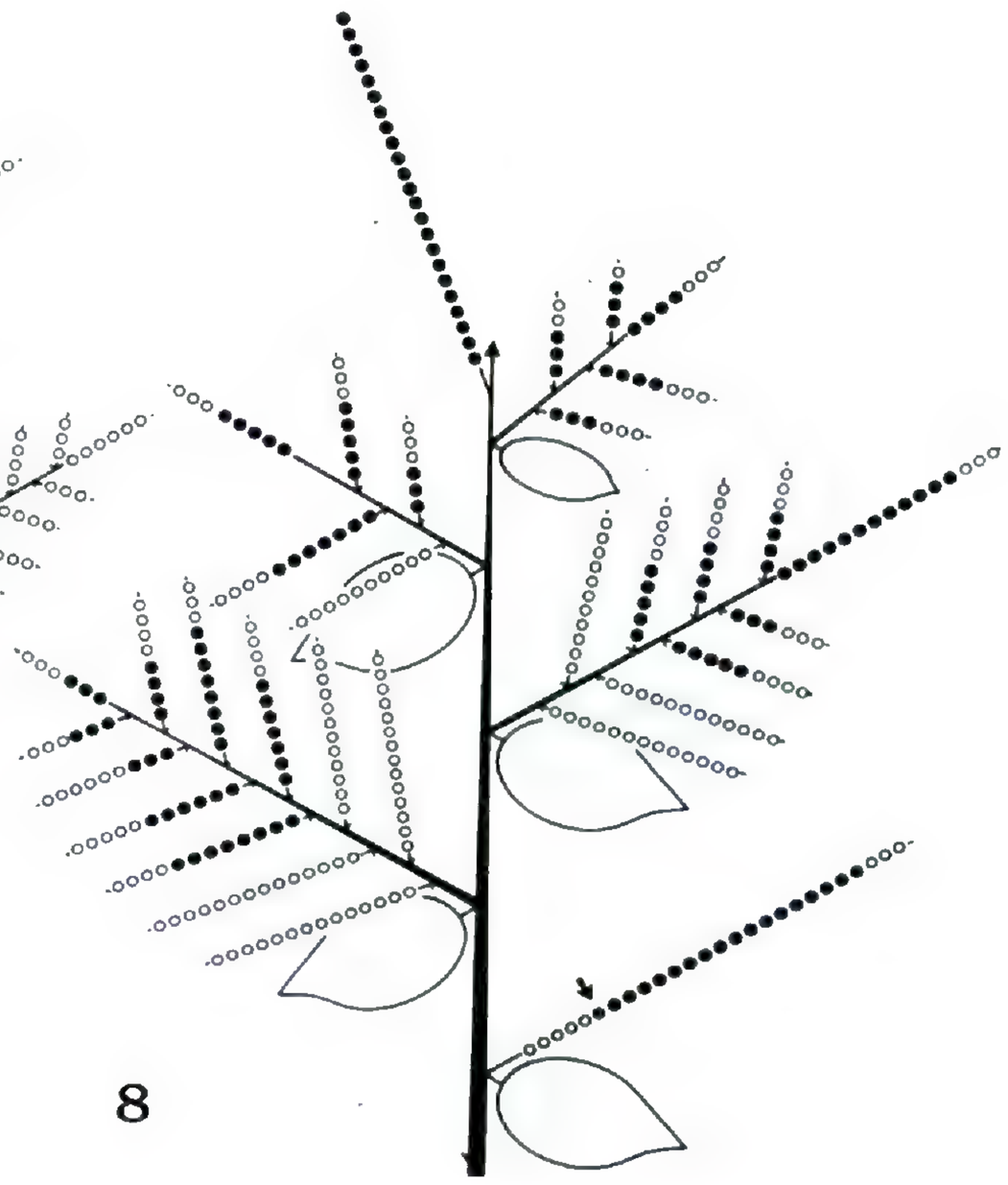




FIGURES 1–5. 1–3. Development of a single flush.—1. Before flush begins. Maturing fruit of previous flush present. Apical bud (triangle) still dormant.—2. End of flush; anthesis. Determinate (without apical bud) and indeterminate (with apical bud) shoots indicated, along with simple and branched spikes. Uppermost spike is androgynous; pistillate dichasia shown in black, staminate as open circles.—3. Post-anthesis. Staminate spikes have fallen, as has the determinate shoot. Fruits of previous flush nearing maturity but those of current flush are immature. Potential succeeding flush stippled.—4. *Lithocarpus elegans* (Bl.) Hatus. ex Soep., from Thailand. Most shoots are indeterminate and one bears a branched spike (left center). Apical bud of the main axis abortive.—5. *L. leptogyne* (Korth.) Soep., from Borneo. Branched spikes are borne on the leader and on the shoots.







FIGURES 6–8. *Lithocarpus*.—6. *L. sundaica* (Bl.) Rehd., from the Malay peninsula. Maturing flush with numerous branched spikes borne on indeterminate shoots. Pistillate spikes have not yet appeared.—7. *L. brevicaudata* Hayata, from Taiwan. New flush approaching anthesis. Each new leaf subtends a branched spike. New pistillate spikes have not yet formed, but those of the previous flush carry maturing fruits and were branched.—8. *L. lampadaria* (Gamble) A. Camus, from the Malay peninsula. Four branched spikes each bear many androgynous branches. The simple spike at the lower right is androgynecandrous and bears one dichasium with both staminate and pistillate flowers (arrow).

(Figs. 4, 16). These proleptic shoots arise from dormant axillary buds at the nodes of the previous flush, whether or not the leaves of that flush are still present.

All determinate axillary reproductive structures, including entire spike- or catkin-bearing shoots, are shed after anthesis except the spikes with pistillate dichasia. Immature fruits of the previous flush are often present at the time of subsequent flushes (Figs. 1–3, 14, 15, 24), a characteristic of tropical species and of some temperate-zone species.

The first nodes beyond the bud scales typically produce only bracts, but these often subtend fertile axes as large as, or even larger than, those axillary to the fully-developed foliage leaves beyond (Figs. 5, 14, 15). Sylleptic shoots usually produce normal foliage at all their nodes.

The floral displays of *Lithocarpus, Castanopsis,* and *Castanea* develop with the new flushes at the branch tips and are therefore easily seen from a distance. Added prominence is given by the somewhat colorful developing leaves in the tropical species. The floral displays are often massive, light in color, and distinctly fragrant and thus attract clouds of insects. The displays of *Quercus* are also often substantial but are drab, odorless, and inconspicuous, especially when hidden among the leaves in evergreen species. In all four genera the pistillate spikes are borne distally in the total inflorescence and are thus exposed.

SPIKES, CATKINS, AND OTHER REPRODUCTIVE BRANCHES

Many species produce spikes that bear only staminate, only pistillate, or various combinations of staminate and pistillate flowers; *Quercus* has only staminate catkins and pistillate spikes. Furthermore, some individuals of some species (except *Quercus*) regularly produce simple spikes whereas others produce more complex structures. For example, only one tree each of *Lithocarpus dealbata* (Fig. 10), *L. elegans* (Fig. 4), *L. harmandii* (Fig. 12), and *L. lampadaria* (Fig. 8) bore branched spikes out of eight, 11, five, and nine trees respectively examined from widely separated areas. Such inconsistency is not confined to inflorescences but is well-known in leaf and even fruit morphology throughout the family. In contrast, most trees of *L. gracilis, L. cooperta* (Fig. 9), *L. brevicaudata* (Figs. 7, 24) and *L. leptogyne* (Fig. 5) had branched spikes.

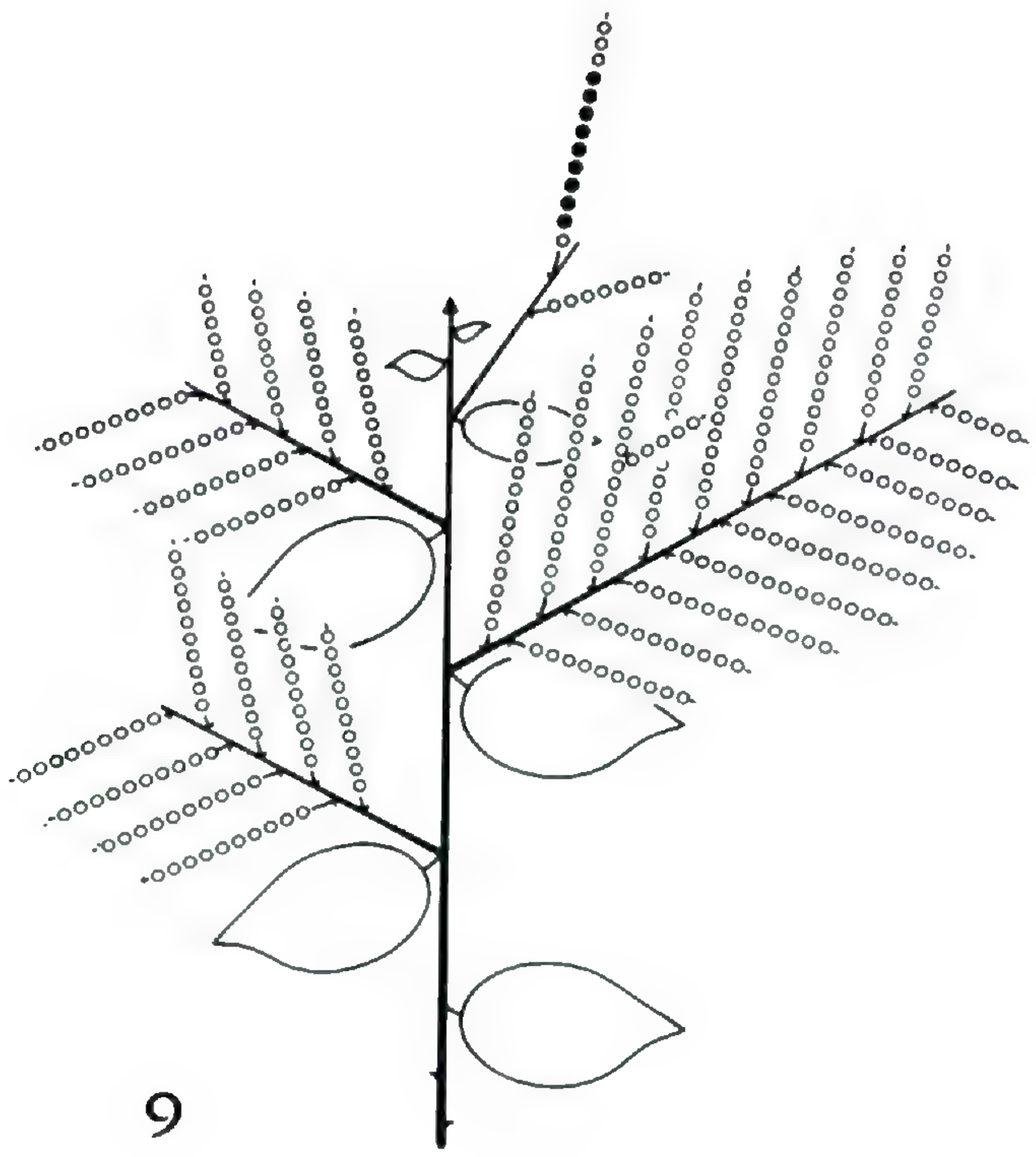
It is obvious from inspection of Figures 4–27 that the structure of reproductive axes varies even on a single shoot. It is common for the extension-growth axes to produce a variety of axillary shoots that are more complex acropetally (Figs. 10, 12, 13) or basipetally (Figs. 5, 6) or medially (Figs. 7, 8, 11). When proleptic reproductive shoots appear synchronously with a new flush, as they usually do, they too are included in these gradients (Figs. 4, 5).

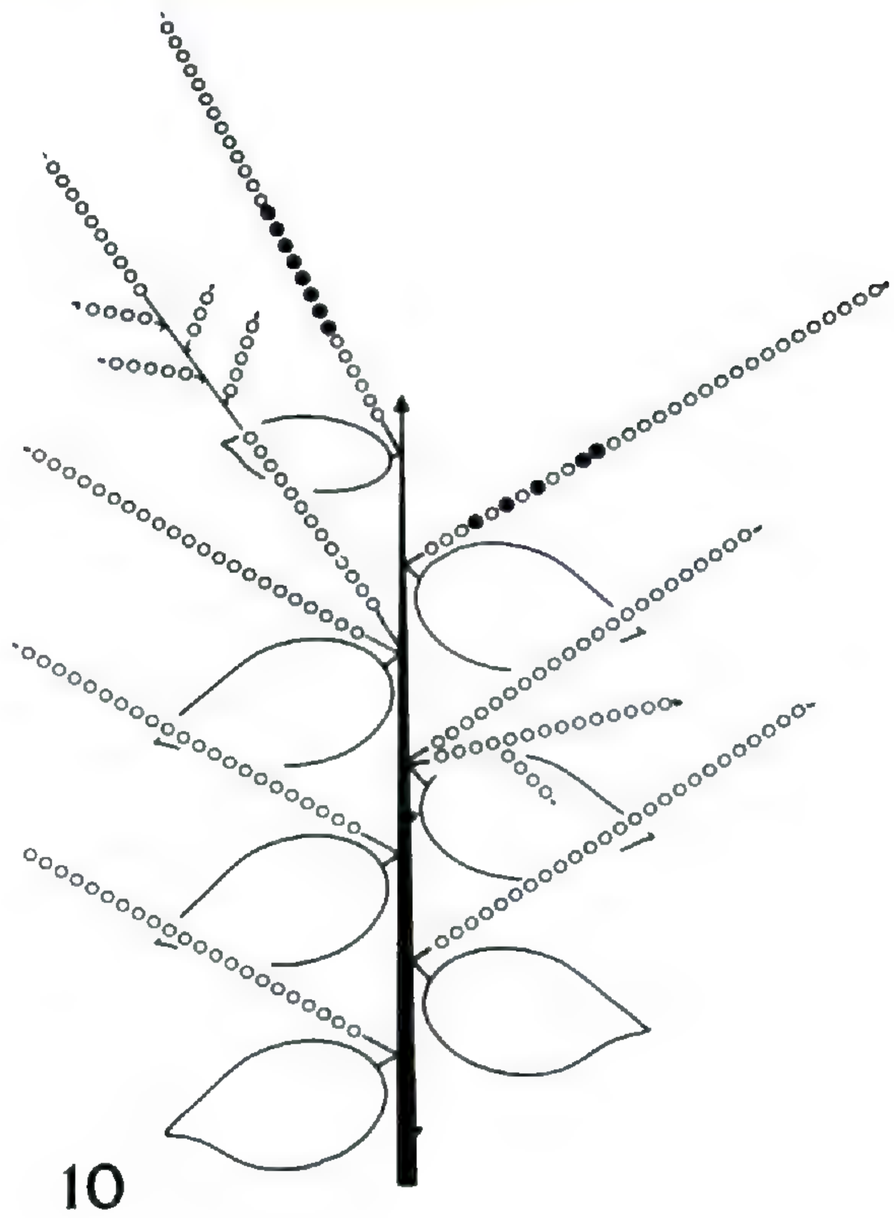
The leader and some reproductive shoots are indeterminate (e.g., Fig. 2) but their apical buds remain dormant until the next flush, by which time the spikes or catkins have fallen. Other reproductive shoots are determinate and produce only spikes (Fig. 2); these entire shoots are often deciduous after anthesis unless they bear pistillate flowers. Determinate shoots must be distinguished from branched spikes; the latter have staminate flowers on the rachis beyond the most distal branch and lack a distinct apical bud, whereas the former clearly terminate in an abortive bud and lack flowers anywhere on the primary axis. In some instances determinate and indeterminate shoots occur, serially, with simple and branched spikes on a branch and the patterns can vary from branch to branch on a tree. Thus the total inflorescence defies classification beyond panicle, sensu lato.

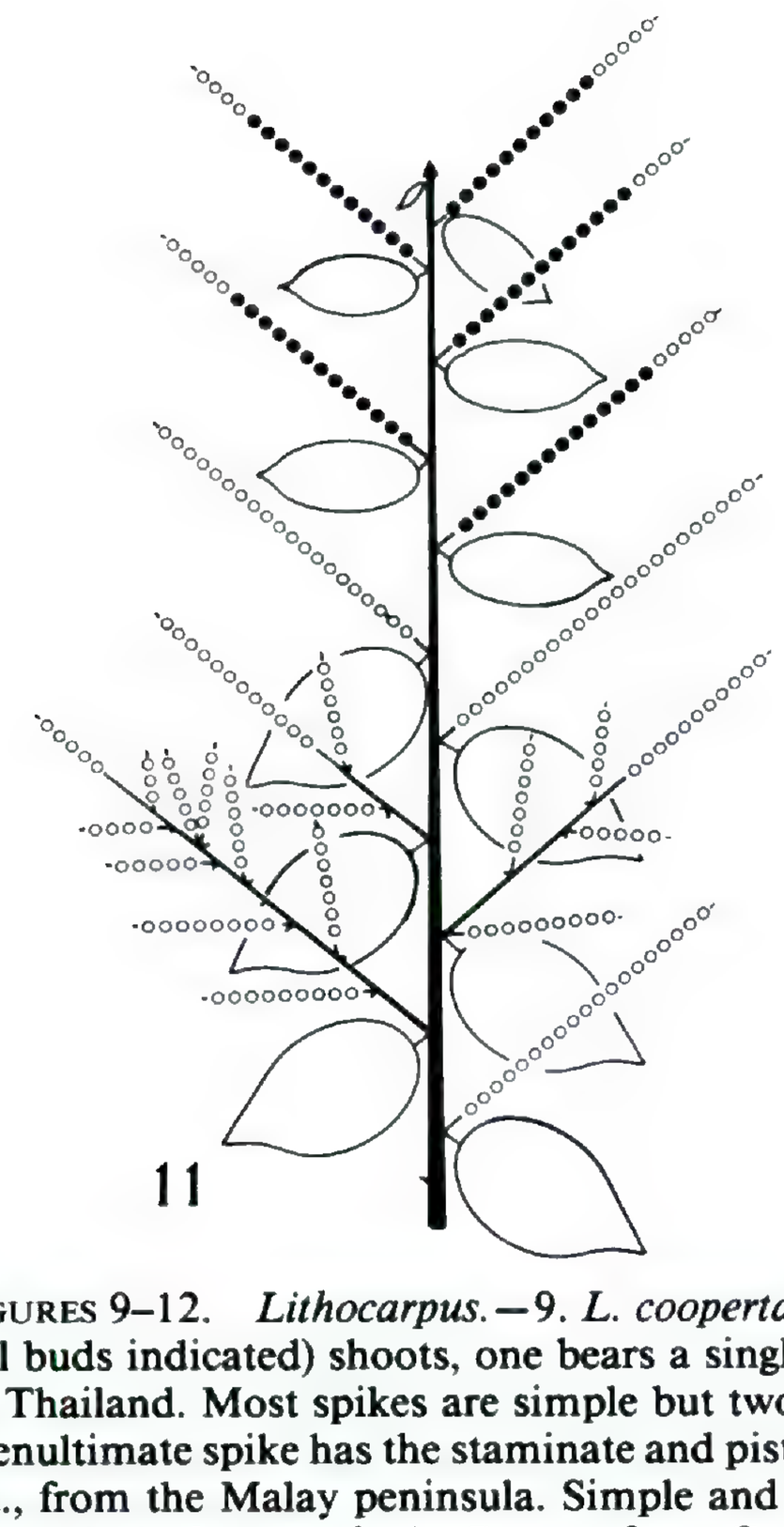
Lithocarpus. Of the four genera, *Lithocarpus* shows the greatest variety of inflorescence modifications. Whereas some species regularly produce branched spikes mixed with simple spikes and various reproductive shoots (Figs. 2–12, 23–25, 27), many, perhaps most, species have simple spikes only, although these may be grouped on shoots that themselves produce massive floral displays (Figs. 25, 27). The patterns approach those of *Quercus* in some species.

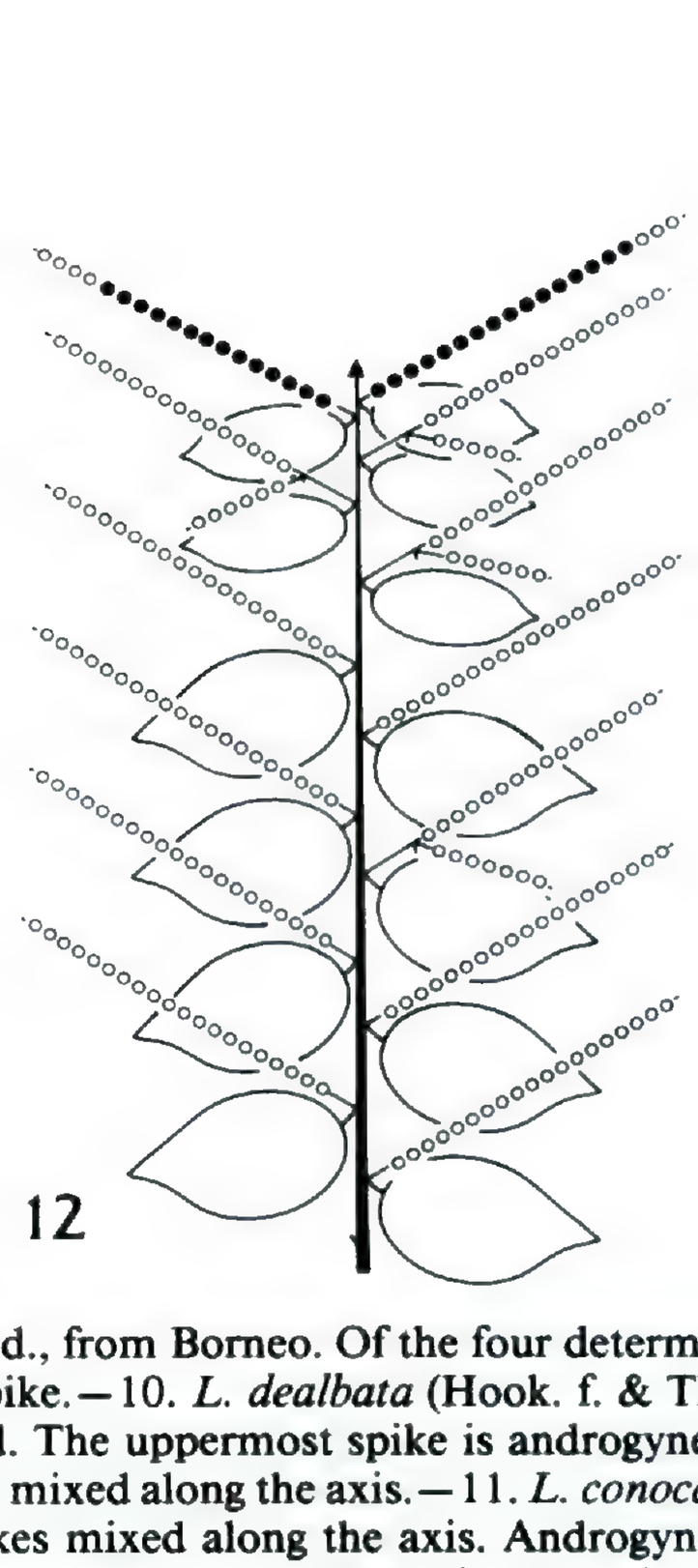
Most of the inflorescence complexity is found in the staminate shoots and spikes but in a few species, for example, *L. brevicaudata* (Figs. 7, 24) and *L. lampadaria* (Fig. 8), the pistillate spikes are branched too. Of the species studied, *L. lampadaria* has the most complex branching of spikes that bear pistillate flowers. In it, large branched spikes bear numerous pistillate dichasia and even more numerous staminate dichasia. Some dichasia include both staminate and pistillate flowers (Fig. 8, arrow) and some spikes have the staminate and pistillate dichasia mixed for short distances (Fig. 20).

The spikes bearing pistillate dichasia in *L.*

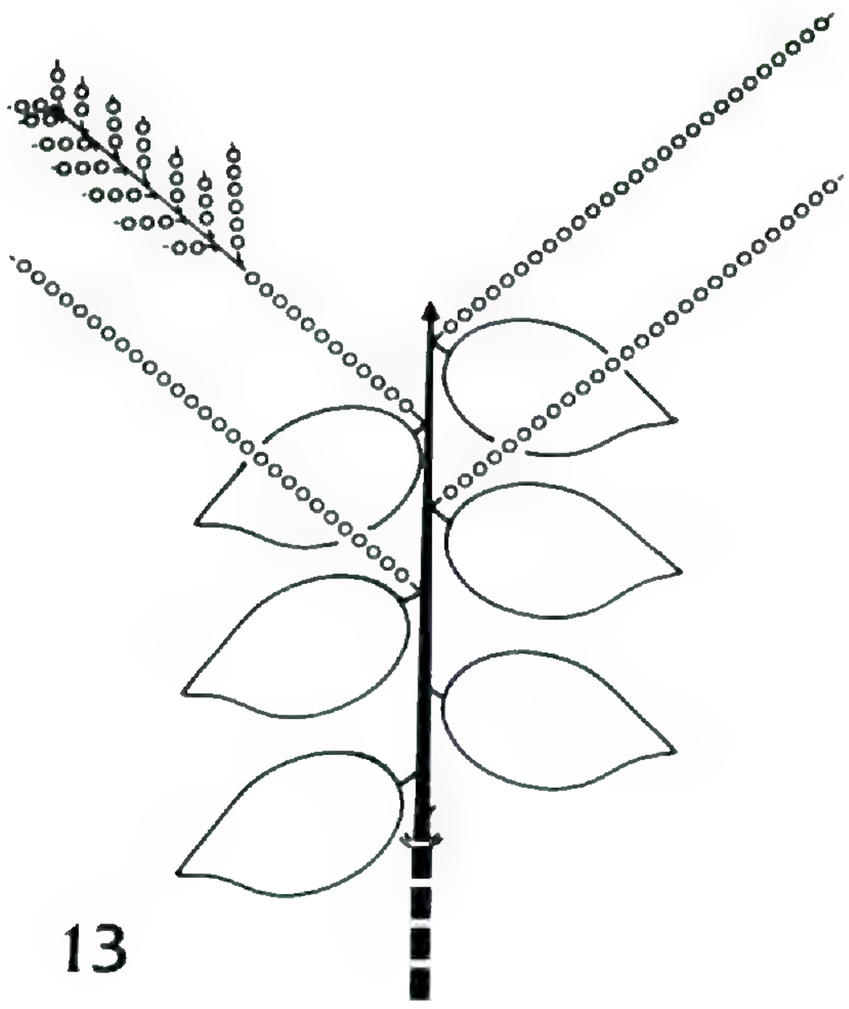








FIGURES 9–12. *Lithocarpus*.—9. *L. cooperta* (Blanco) Rehd., from Borneo. Of the four determinate (without apical buds indicated) shoots, one bears a single branched spike.—10. *L. dealbata* (Hook. f. & Thoms.) Rehd., from Thailand. Most spikes are simple but two are branched. The uppermost spike is androgynecandrous and the penultimate spike has the staminate and pistillate dichasia mixed along the axis.—11. *L. conocarpa* (Oudem.) Rehd., from the Malay peninsula. Simple and branched spikes mixed along the axis. Androgynous spikes are distal.—12. *L. harmandii* A. Camus, from Cambodia. Most spikes are simple but four staminate spikes each bear a single branch.



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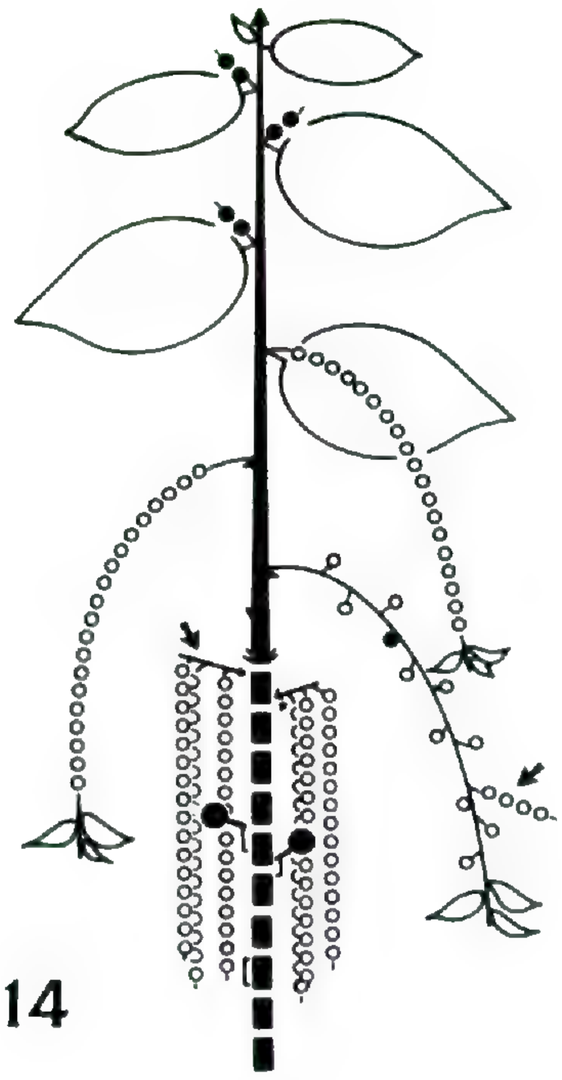

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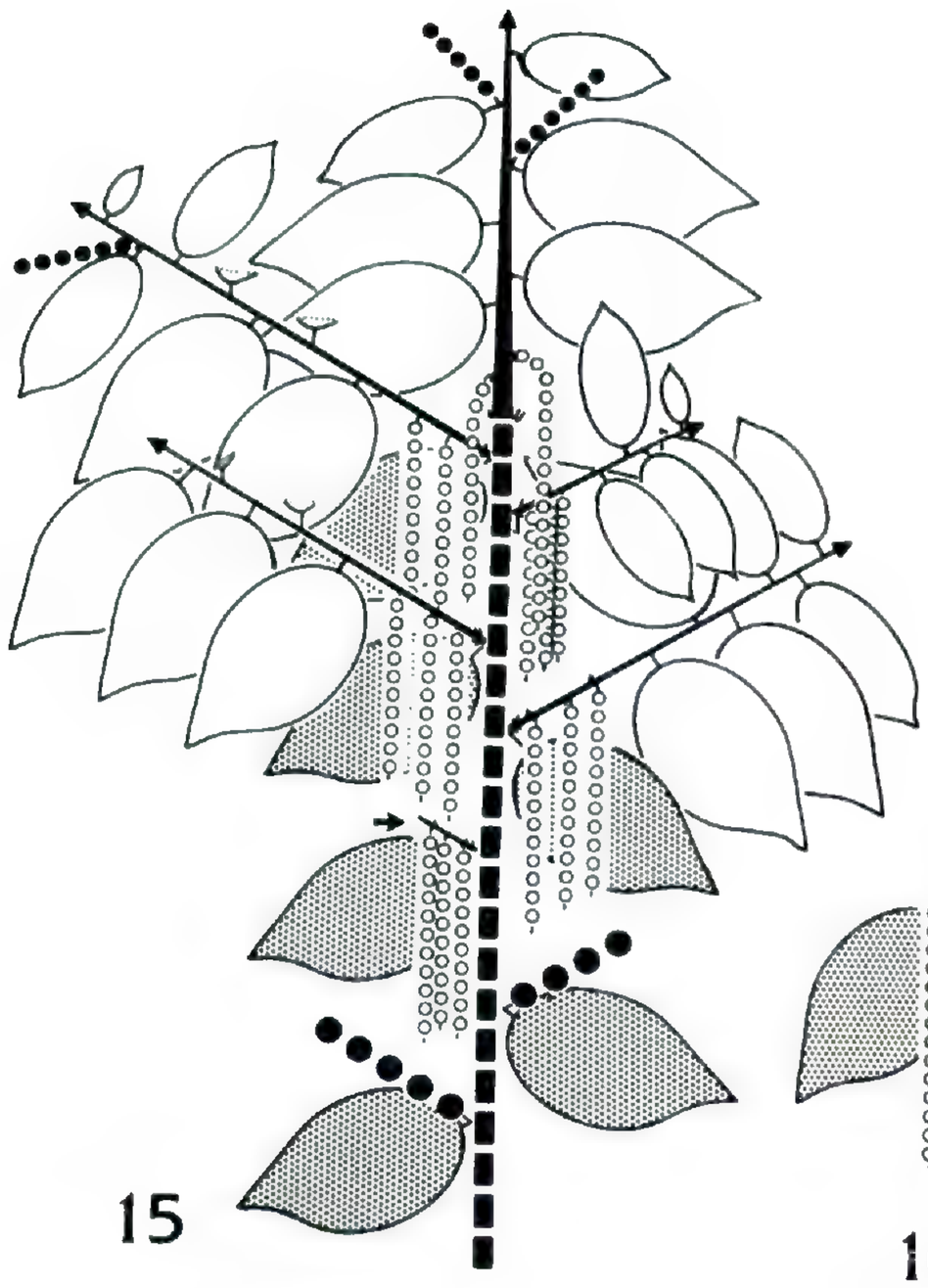

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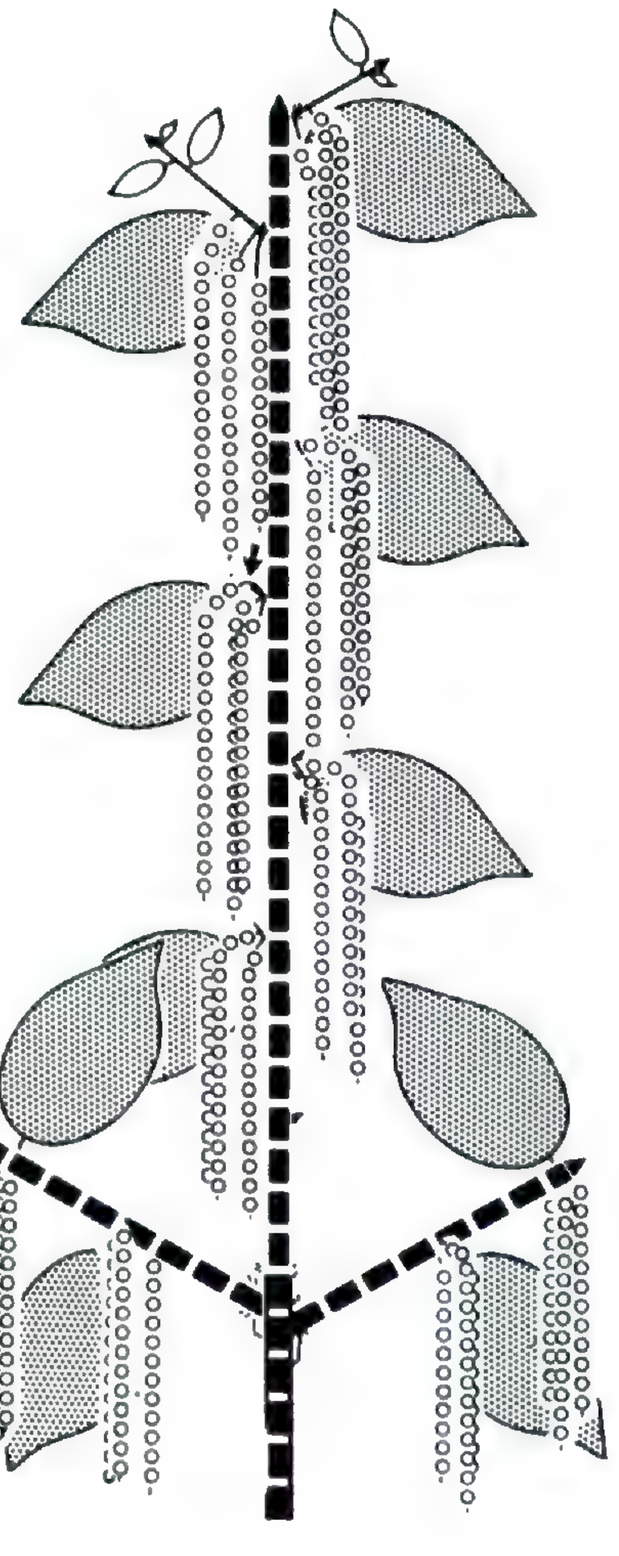

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FIGURES 13–16.—13. *Castanea crenata* Sieb. & Zucc., from Taiwan (cultivated). The uppermost dichasia of one spike are replaced by staminate branches.—14. *Quercus marilandica* Muenchh., from Nebraska. Branch from a tree that annually bears proliferative catkins and branched catkins (right arrow). Left arrow indicates a staminate short-shoot that emerged from a bud of the previous flush.—15. *Q. pachyloma* O. Seem., from Taiwan. Typical inflorescence for many *Quercus* species. Proleptic indeterminate long-shoots are basally floriferous and the uppermost one, as well as the leader, bears pistillate spikes. One staminate short-shoot (arrow) is shown.—16. *Q. gilva* Blume, from Taiwan. Although the new flush has barely begun to produce extension growth, each leaf of the previous flush has produced a proleptic, staminate short-shoot in its axil.

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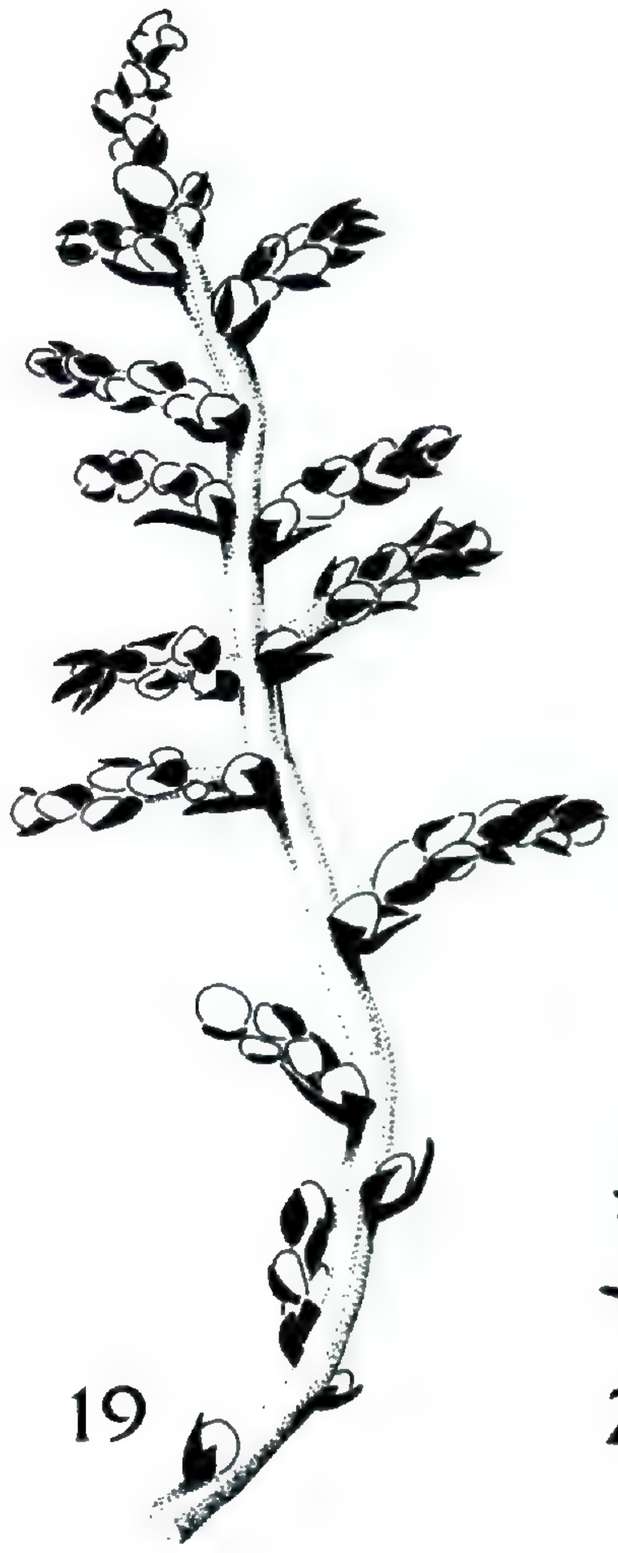
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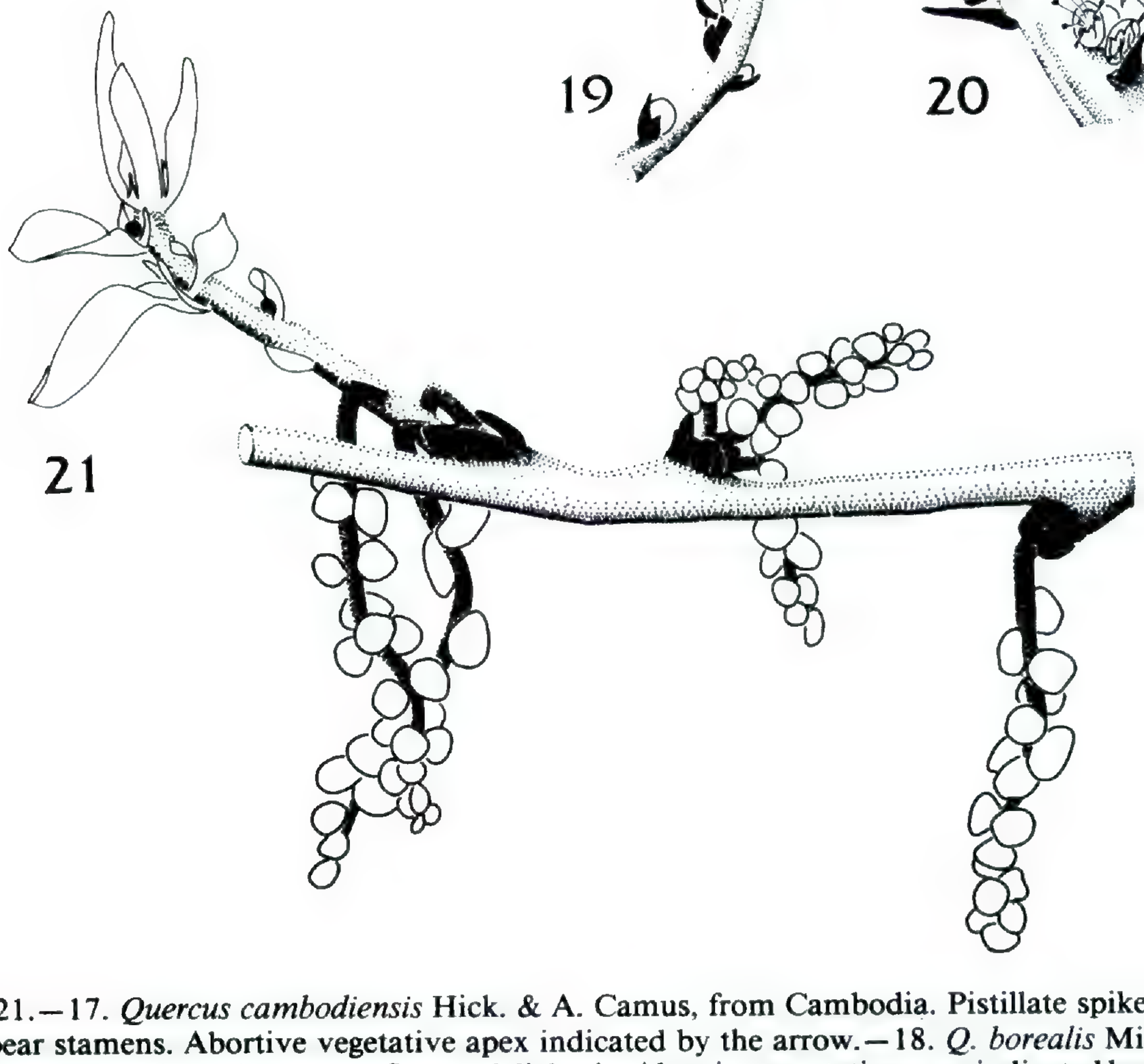
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FIGURES 17–21.—17. *Quercus cambodiensis* Hick. & A. Camus, from Cambodia. Pistillate spike in anthesis. Some flowers bear stamens. Abortive vegetative apex indicated by the arrow.—18. *Q. borealis* Michx. f., from Nebraska. Pistillate spike with only two one-flowered dichasia. Abortive vegetative apex indicated by the arrow.—19. *Lithocarpus brevicaudata* branched spike just before anthesis.—20. *L. lampadaria,* from the Malay peninsula. Portion of spike showing mixed staminate and pistillate dichasia.—21. *Quercus chapmanii,* from Florida. Stem segment showing long-shoot (left) and two short-shoots, one of which bears a single catkin. Pistillate spikes are forming in two leaf axils.

FIGURES 22–25.—22. *Castanea crenata* Sieb. & Zucc. Arrow indicates one of two pistillate dichasia on that spike. Two other spikes have a single basal pistillate dichasium and four spikes are entirely staminate.—23. *Lithocarpus sundaica* (Blume) Rehder. Arrow shows a branched spike. No pistillate spikes are visible. Some leaves have fallen.—24. *L. brevicaudata* Hayata showing prominent branched spikes.—25. *L. neorobinsonii* A. Camus. Arrow indicates an indeterminate reproductive branch whose apical bud is barely visible. Below it, on the right side of the stem, is a determinate reproductive branch. Maturing fruits of the previous flush are shown.

brevicaudata are simpler; only the distal one or two spikes have pistillate flowers and are sometimes branched (Fig. 7). Each branch of the spike is androgynous, as is the case in *L. lampadaria.* Irrespective of the complexity of branching in these species, the pistillate dichasia are most abundant distally in the total inflorescence.

A variety of branching patterns in the staminate spikes and shoots is shown in Figures 4–7, 9–12, 19, 23–25, where there is a seemingly random interchangeability of simple with branched spikes on both the leader and lateral axes. Again the gradient of complexity is neither acropetal nor basipetal in the genus as a whole but apparently varies, even on the individual tree. In some cases illustrated, the branched spikes are more abundant acropetally (Figs. 9, 10, 12) or basipetally (Figs. 6, 11) but elsewhere they are borne throughout (Fig. 7).

Some spikes are unbranched, some have one branch (Figs. 6, 9, 12), and some have many (Figs. 7, 19, 24). Sometimes staminate dichasia occur directly on the primary axis among or below the branches (Figs. 6, arrow; 19). The branches of the spikes occur at dichasial nodes and are subtended by the same bract pattern as the dichasia (Fig. 19).

The single New World species of *Lithocarpus, L. densiflora* (H. & A.) Rehd., regularly exhibits a few branched spikes (Kaul & Abbe, 1984), suggesting that this long-isolated species has retained this primitive character state.

Castanopsis. There is less variability in inflorescence structure in *Castanopsis* than in *Lithocarpus.* Of the 41 species examined, only the single New World representative, *C. chrysophylla* (Dougl.) A. DC., has even an occasional branched spike (Kaul & Abbe, 1984, fig. 38). All others produce determinate and indeterminate shoots bearing simple spikes (e.g., Fig. 26) in patterns like those of *Lithocarpus.*

Castanea. Of the five species of *Castanea* examined (*C. crenata, C. dentata, C. mollissima, C. pumila,* and *C. sativa*) only *C. crenata* bears branched spikes (Fig. 13), which are only occasional even in this species. However, a given tree sometimes produces them abundantly. Most spikes are simple and staminate (Fig. 13) but some of the more distal spikes often bear a few proximal pistillate dichasia (Fig. 22, arrow).

Quercus. The pistillate spikes are always simple and borne singly in the axils of the most distal leaves (Fig. 15). They have one to ten or more dichasia (Figs. 15, 17, 18), each reduced to a single functional flower. Generally, the lowland paleotropical species have more pistillate dichasia per spike than do the montane and northern species. Occasionally a few staminate flowers are present on the spike, and often there are perfect flowers (Fig. 17). The vestigial vegetative apex is frequently prominent (Figs. 17, 18, arrows).

The catkins are always staminate (except in distinctly aberrant instances) and are borne on both long- and short-shoots. On the long-shoots they are commonly produced singly in the axils of the lower bracts (Figs. 15, 21), but they sometimes occur in leaf axils as well. Short-shoots appear singly and proleptically at the nodes of the stem of the previous flush (Figs. 14–16, arrows; 21). They carry one to ten catkins and are invested at the base with the bracts of the bud that enclosed them (Fig. 21). Most short-shoots abscise soon after anthesis but a few eventually elongate and produce leaves. Figure 21 shows part of a branch that bears short- and long-shoots with catkins; one short-shoot has but a single catkin whereas another has three, as does the long-shoot.

Figure 15 illustrates the typical condition in *Quercus.* Pistillate spikes are borne in leaf axils of the leader and (often) one or a few of the most distal proleptic branches. Catkins appear on all the long-shoots of the current flush as well as on the short-shoots. Because Figure 15 illustrates an evergreen species, leaves of the previous flush are shown. Most leaves are sterile at the time they appear, except for those that subtend pistillate spikes, but many leaves will subtend axillary long- or short-shoots in the next flush.

Figure 16 illustrates a rather common phenomenon in paleotropical *Quercus*: the appearance of proleptic, reproductive short-shoots before significant extension growth occurs. The extension growth also bears some catkins and all the pistillate spikes. However, some such protandry (at the inflorescence level) occurs in more northerly species too, insofar as they display at least some catkins in anthesis before the pistillate flowers are receptive.

Branched catkins (equivalent to the branched spikes of the other three genera) are occasional in many species but somewhat common in a few. For example, *Q. elmeri* of Borneo has a few on some trees and *Q. marilandica* of the southeastern United States regularly produces them on an

FIGURES 26–28.—26. *Castanopsis cuspidata* Schottky. Simple staminate spikes are borne singly in the axils of most new (darker) leaves.—27. *Lithocarpus dealbata* (Hook. f. & Thomson) Rehder showing simple staminate spikes, some of them on indeterminate branches (obscured). The upper two spikes bear some pistillate and

occasional tree. Figure 14 illustrates a branched catkin in the latter species, from a tree that was observed to produce them regularly for nine years. Most of the catkins are simple, whether or not they are borne on the current flush's long- or short-shoots. Some of the catkins, although unbranched, are somewhat indeterminate in that they proliferate beyond the floriferous region and develop a few small leaves; after anthesis the dichasia drop from these proliferative catkins but the axis and leaves persist. An occasional proliferative catkin is also branched (Fig. 14, right arrow) and sometimes bears one or two pistillate dichasia.

Discussion

The multiplicity of branching patterns of staminate spikes and shoots, particularly in *Lithocarpus,* shows that at least in some species flexible and variable patterns are the normal condition. The simple, unisexual spike or catkin is the advanced state in the family and occurs in most species, but a few species have retained branched spikes that suggest more complexity in ancestral forms of the genus. Of the four genera considered here, *Lithocarpus* has not only the most primitive inflorescences but also, according to Soepadmo (1972), the least specialized dichasia. The other genera, and especially *Quercus,* have achieved more stability in inflorescence structure and have only occasional inflorescences suggestive of more complex ancestry. Not only does *Quercus* have complete separation of pistillate from staminate function in most species, but it also bears the determinate reproductive shoots (short-shoots in this case) only proleptically, in contrast with *Lithocarpus,* in which such shoots occur both sylleptically and proleptically. In *Quercus,* the spikes bearing pistillate flowers are morphologically very distinct from the catkins and well removed from them. In *Lithocarpus, Castanea,* and *Castanopsis,* by contrast, the pistillate flowers usually share a spike with at least a few, and often with very many, staminate flowers. Therefore, I conclude on morphological grounds, by employing the concepts of assessing evolutionary advancement by, among other things, the degree of spatial separation of staminate from pistillate functions, that *Quercus* is the most advanced of the four genera.

Separation of staminate from pistillate functions has not yet progressed to dioecy in these genera. In fact, many species have morphologically (if not functionally) perfect flowers, including a few *Quercus* species, and mixed-sex dichasia are frequent in *Lithocarpus* and *Castanopsis* (Kaul & Abbe, 1984). This contrasts with two putatively related families, Betulaceae and Juglandaceae, in which monoecy is clearly established. Those families are entirely anemophilous but only *Quercus* is, of the four fagaceous genera studied here, and it shows the closest approach to monoecy. This adds to the extensive evidence that monoecy (and also dioecy) is characteristic of anemophilous trees. Thus the Fagaceae can be interpreted as having some transitional stages from perfect, entomophilous flowers to imperfect, anemophilous flowers and from mixed-sex spikes to unisexual spikes.

Homologies of staminate and pistillate spikes are indicated by numerous and frequent transitional forms, especially in *Lithocarpus* and *Castanopsis.* The relationships of simple to branched spikes and of the spikes to reproductive shoots are also clarified by the presence of intermediates, even on a single shoot system. Furthermore, every transitional stage between strictly staminate and strictly pistillate dichasia can be found, especially in *Lithocarpus,* and both of those extremes must be considered ultimate modifications. While the staminate dichasia do not have an obvious cupule like that of the pistillate dichasia, there are suggestions of a cupular homologue in the abundant bracteation that characterizes some of them (Kaul, in prep.).

The branches of the branched spikes occur at the sites of dichasia and, in fact, even have the same basal bracteation as the dichasia. Evolution of the simple spike can be interpreted as loss of branching capacities in the branched spikes. (The opposite change is not impossible: reactivation of meristems in dichasia could produce branched from simple spikes.) Such a loss seems consistent with the losses of flowers and internodal elon-

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staminate dichasia, the point of separation between the distal staminate and proximal pistillate dichasia being indicated by the arrow.—28. *L. suffruticosa* (Ridl.) Soep. with two mature pistillate spikes. Typically, not all pistillate flowers develop fruit.

gation that occurred during evolution of the individual dichasium. The interchangeability of branches with dichasia suggests that the dichasia (both staminate and pistillate) are the result of evolutionary condensation of branches.

Most of the critical work on the reproductive biology of inflorescences has been done on herbaceous plants [see Wyatt (1982) for a review] but there is no reason to suspect that the principles emerging from those studies would not apply to trees. Such research in the Fagaceae might help to explain such things as miniaturization of flowers and the accompanying evolution of the cupule, the failure of the family to advance to dioecy despite its antiquity, and the instability of inflorescence patterns in some species. Also of interest is the adaptive value of the formation of the pistillate flowers distal to the staminate (so pronounced in the Fagaceae), which is common in both the anemophilous and the entomophilous monoecious dicotyledons (but not in the monocotyledons, where the opposite condition prevails). Furthermore, such studies could help to explain the factors involved in the change from entomophily to anemophily in the Fagaceae, a topic reviewed for plants in general by Regal (1982) and Whitehead (1983) and broached for the Fagaceae by Kaul et al. (1986) but in need of substantially more research.

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FLORAL STRUCTURE, SYSTEMATICS, AND PHYLOGENY IN TROCHODENDRALES[1]

PETER K. ENDRESS[2]

ABSTRACT

Study of the floral structure of *Cercidiphyllum, Euptelea, Tetracentron,* and *Trochodendron,* at anthesis and in earlier developmental phases, revealed new features of macrosystematic interest. They include the presence of rudimentary tepals in *Trochodendron,* and valvate anther dehiscence, similar exine structure, and similar nectaries on dorsal carpel bulges in *Trochodendron* and *Tetracentron.* These and other similarities point to a close relationship between *Trochodendron* and *Tetracentron,* which together are formally best treated as a family Trochodendraceae. Other new characters, such as zygomorphy or bilateral symmetry of the flowers in early developmental phases and relatively similar anther differentiation, in addition to the established similarities, corroborate the relative homogeneity of the four genera, which can be seen as members of a single order Trochodendrales. The position of this order is intermediate between the Magnoliidae and Hamamelidae so that the formal inclusion of the order in either group can be justified.

The four unusual eastern Asiatic genera *Cercidiphyllum, Euptelea, Tetracentron,* and *Trochodendron,* with only six species among them are systematically isolated from other dicots, but they form a homogeneous group. This is more or less generally accepted today. In recent classifications they appear in the same order Trochodendrales or at least in the same subclass Hamamelidae. This was not always the case, and their taxonomic history sheds some light on their systematic and phylogenetic significance.

The outstanding combination of characters such as vesselless wood, lack of a perianth, and a special kind of triaperturate pollen make them intermediate between the Magnoliidae and the Rosidae-Hamamelidae. Therefore, the views on the systematic position of the group have oscillated between magnolialian and hamamelidalian affinities.

Siebold and Zuccarini (1839) described the first genus *Trochodendron* and placed it in the Winteraneae. Oliver (1889) described the last of the four genera, *Tetracentron,* and put all of them in the tribe Trochodendreae of the Magnoliaceae.

But Baillon (1871) had already proposed that *Cercidiphyllum* might have affinities with the Hamamelidaceae. Solereder (1899) corroborated this suspicion by extensive morphological work, and Hallier (1901, 1903a, 1903b, 1904) very vividly put forward that Trochodendraceae also are very near the Hamamelidaceae and should even be included in them.

The pendulum swung back with I. W. Bailey and his coworkers, who carefully studied all four genera and firmly established the relationship with the Ranales (Magnoliideae) (Bailey & Nast, 1945; Nast & Bailey, 1945, 1946; Swamy & Bailey, 1949). Pervukhina (1963) and Endress (1969) were of the same opinion after comparative developmental studies of *Trochodendron* and *Euptelea,* respectively.

But the present tendency is to include all four genera in Hamamelidae (Takhtajan, 1964, 1983; Smith, 1972; Cronquist, 1981) (or Hamamelidales sensu Thorne, 1983); *Trochodendron* and *Tetracentron* in Trochodendrales, and *Euptelea* and *Cercidiphyllum* in Hamamelidales (Cronquist, 1981). Dahlgren (1980, but not 1983) placed the four genera in the Trochodendrales. Every genus is in a separate family or even in a separate order (as in Takhtajan, 1983).

Thus, the gross systematic history from the beginning until now shows a change in the emphasis from magnolialian to hamamelidalian affinities. Both are somewhat one-sided positions, because there are clearly affinities to both groups, and the new results presented here corroborate this view. However, for purposes of classification

[1] I thank B. L. Burtt, Royal Botanic Garden, Edinburgh, for providing fixed material of *Tetracentron sinense,* and U. Jauch, Institut für Pflanzenbiologie, University of Zürich, R. Siegrist, and A. Zuppiger for technical collaboration. I am grateful for valuable comments on the manuscript by Nancy R. Morin, Rudolf Schmid, and Shirley C. Tucker.

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it is necessary to place them in only one of the groups, but placement either way can be about equally justified.

MATERIALS AND METHODS

The following collections, all cultivated material, were used for this investigation:

Cercidiphyllum japonicum Hoffmann et Schultes, male, *Endress 6687* (dat. div., 1984); female, *Endress 6688* (dat. div., 1984), old Botanical Garden, University of Zürich.

Euptelea polyandra Sieb. et Zucc., *Endress 516* (dat. div., 1967–1968), Eidgenössische Forschungsanstalt für Obst-, Wein- und Gartenbau, Wädenswil (Figs. 3, 32, 40, 44, 58, 59); *Endress 6686* (dat. div., 1984), Botanical Garden, University of Zürich (all other figures).

Tetracentron sinense Oliver (8 June 1976, 10 Aug. 1976), Royal Botanic Garden, Edinburgh.

Trochodendron aralioides Sieb. et Zucc., *Endress 6684* (dat. div., 1984), Botanical Garden, University of Zürich.

All material is deposited in Zürich (Z). Figures 32 and 40, where only the generic name is mentioned, are both based on these species and specimens.

Flowers at anthesis and in various developmental stages were observed in the living state (except *Tetracentron*). Material fixed in FAA of all four genera was studied with serial microtome sections stained with safranin and astra-blue and with the scanning electron microscope after treatment with the critical-point drying and Au/Pd-sputtering methods.

RESULTS

THE FLOWERING SHOOT AT ANTHESIS

There is a differentiation in long and short shoots with inflorescences produced only on short shoots, except in *Trochodendron*. This differentiation is most extreme in *Cercidiphyllum* and *Tetracentron*, both having short shoots with a single foliage leaf.

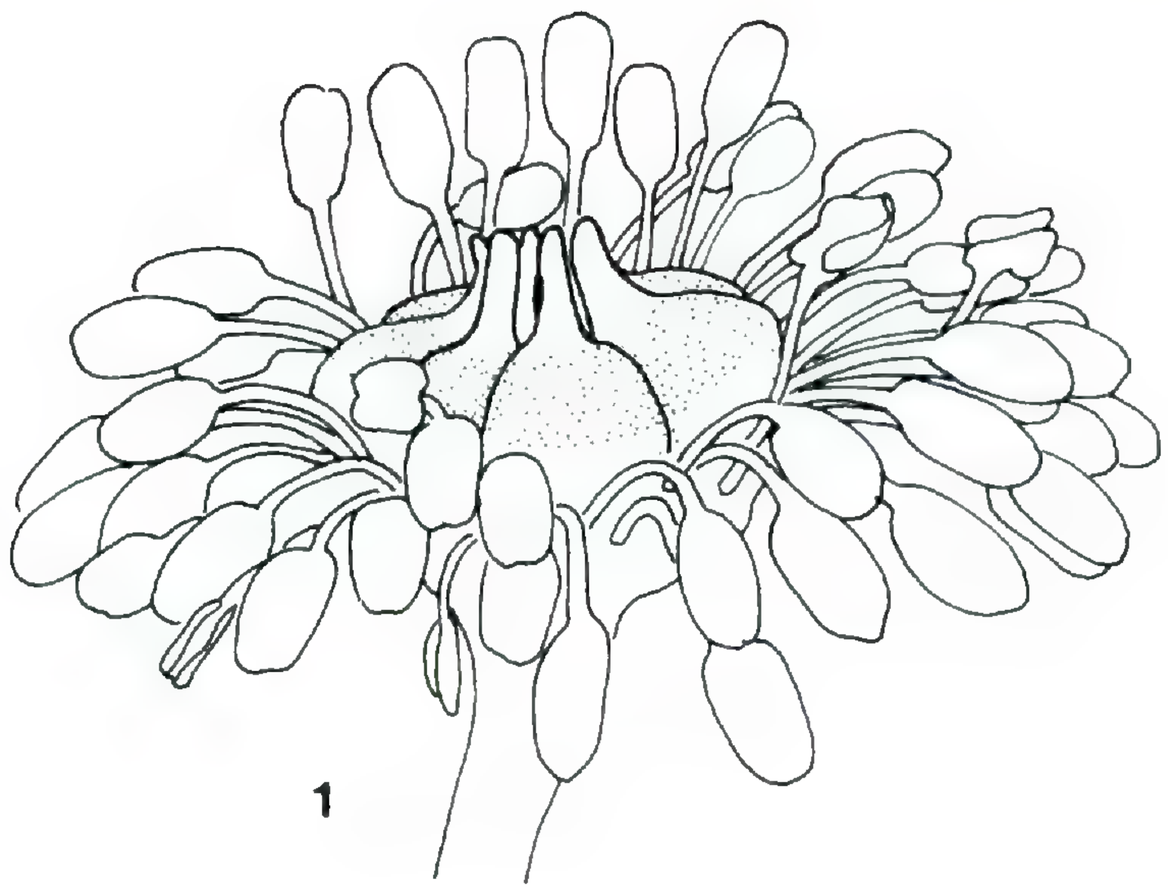
Trochodendron. An upright cluster of 10–30 yellowish green bisexual flowers (ca. 1 cm diam.) (Fig. 1) with long pedicels appears in late spring while the shoots are expanding. Flowers observed in the Botanical Garden at Zürich in 1980 became visible between the bud scales and leaves in early May. On 12 May the flowers were all exposed, on 22 May open nectar was present between the stamens and styles on the ovary surface, but all anthers were still closed. On 28 May the first stamens were open and contained sticky pollen; dry remains of nectar were still present. During the period when they were fully exposed, the open flowers enlarged from about 0.8 to 1.2 cm diam.

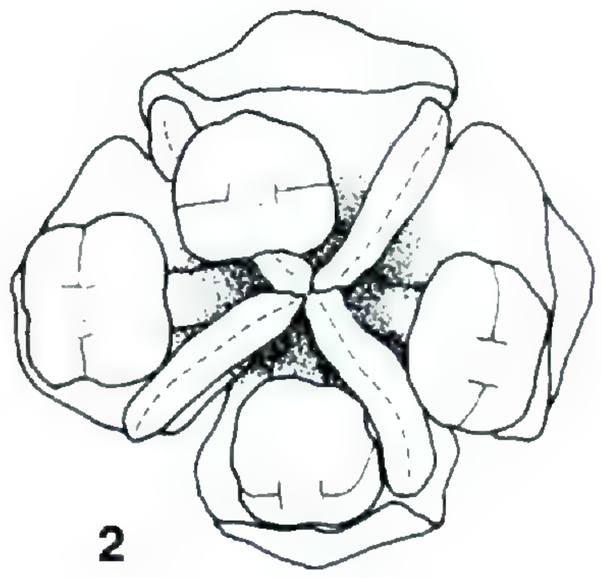
Since mature fruits regularly developed from that plant, the flowers seem to be bisexual (or the development may be apomictic). The flowers seem to be proterogynous. There is no sign of androdioecism in contrast to the observation of Keng (1959) on plants in Taiwan. The floral character syndrome points to myophily (or unspecialized entomophily). Keng (1959) observed bees and butterflies as visitors of the sweet-scented flowers in mid-April 1957 in Taiwan.

Tetracentron. About a hundred very small yellowish bisexual flowers (2 mm diam.) (Fig. 2) are sessile on a long stiff axis. The studied material, cultivated in Edinburgh, flowered in late summer (August 1976). A secretory surface that apparently also secretes nectar is at the same site as in *Trochodendron*. Presumably the flowers are also myophilous (Takhtajan 1969; Cronquist 1981: anemophilous).

Euptelea. A cluster of 6–12 (Smith, 1946) pendent inconspicuous bisexual pedicelled flowers with many stamens and carpels (Fig. 3) is produced by each flowering shoot. In the closed state the long anthers are red, but brownish when open. Pollen is dry and powdery. The minute carpels expose the white stigmatic papillae between the filament bases. No nectar is produced. In contrast to *Trochodendron*, anthesis is short and takes place in early spring (March or April at Zürich) before the young leaves expand. Thus, *Euptelea* exhibits an anemophilous character syndrome. *Euptelea polyandra* is presumably at least partly self-incompatible. Two neighboring specimens cultivated in the Botanical Garden at Zürich regularly set copious fruit, but other plants cultivated in isolation produce few or no fruits.

Cercidiphyllum. This is the only genus of Trochodendrales with unisexual flowers (in dioecious distribution). The inconspicuous female inflorescences consist of two to seven (Spongberg, 1979) unicarpellate flowers with big red stigmas (Fig. 4a). The likewise inconspicuous male inflorescences produce a cluster of about 25–32 (up to 40 according to Spongberg, 1979) long pink anthers on slender, pendulous filaments (Fig. 4b). The flower number is difficult to determine (see section on floral ontogeny). The opening anthers turn brownish and present co-

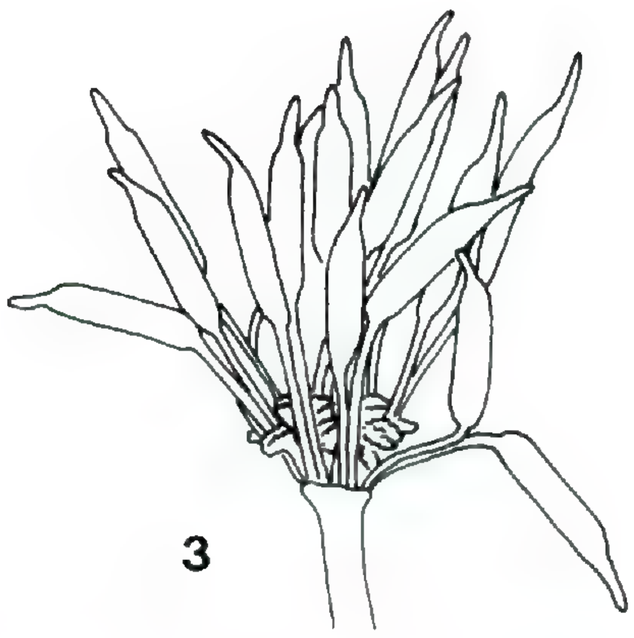


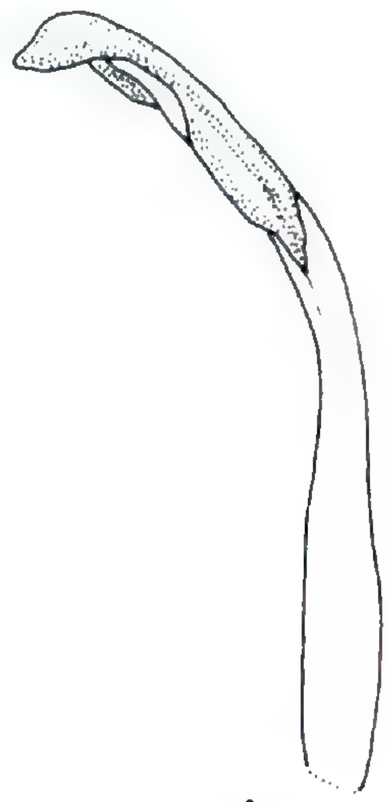


1mm
2

1mm
1, 4a

1mm
3,4b





FIGURES 1–4. Flowers at anthesis.—1. *Trochodendron aralioides,* nectary stippled.—2. *Tetracentron sinense.*—3. *Euptelea polyandra.*—4. *Cercidiphyllum japonicum*: a, female flower, stigma stippled; b, entire male inflorescence.

pious powdery dry pollen. Nectar is lacking. As in *Euptelea,* anthesis is short in early spring before shoot expansion (March or April at Zürich). The anemophily syndrome is obvious.

PERIANTH

One of the oddities of the Trochodendrales is that the flowers lack a perianth. The only exception is *Tetracentron* with a perianth of four tepals. This was the main reason why *Tetracentron* has been, at times, removed from the other three genera, such as by Harms (1897), who put *Tetracentron* in Magnoliaceae but the other genera in Trochodendraceae.

However, the situation is more complicated. Developmental studies have allowed new insights. For a better understanding of the perianth, an analysis of the entire inflorescence is necessary.

Tetracentron. In morphological terms the inflorescence is a spike (at times with a terminal flower, according to Nast & Bailey, 1945, but not present in my material). Each flower sits in the axil of a subtending bract (= pherophyll in the terminology of Briggs & Johnson, 1979). The four tepals cover the inner floral organs in bud. They are not arranged in a whorl, but in two alternate pairs. The first pair has a transversal position similar to that of the two floral prophylls in many dicots (Fig. 5). In *Tetracentron,* there are no prophylls outside the tepals, but the two outer tepals correspond to prophylls in respect of their position. In correlation with their diminished size—the entire flowers being minute—and thin texture, the tepals often lack well-differentiated vascular bundles (cf. also Nast & Bailey, 1945). An interesting detail are cushions with small, but radially elongated thin-walled epider-

mal cells at the inner base of the tepals (Fig. 6). Presumably they play a role in the opening movement of the tepals.

Trochodendron. The inflorescence is a raceme, usually with a terminal flower ("botryoid" in the terminology of Troll, 1964; see also Briggs & Johnson, 1979). In rich inflorescences the lowermost lateral branch may bear one or more secondary lateral flowers; they are, then, incipient panicles. The lateral flowers of the raceme have two tiny prophylls in a transversal position (Figs. 7–9, 11–13); they are somewhat larger on the lowermost lateral flower (Figs. 14–16). Between the uppermost lateral flower and the terminal flower there are a few scales (Wagner, 1903; Nast & Bailey, 1945; Melville, 1969; Cronquist, 1981) (Fig. 17). They are serially homologous to the subtending bracts (pherophylls) of the lateral flowers on the main inflorescence axis. This is a feature that often occurs in botryoids and has nothing to do with a perianth ("Zwischenblätter," Troll, 1964; "metaxyphylls," Briggs & Johnson, 1979). Thus, there are no obvious tepals, as recorded in the literature.

However, in studying young stages of *lateral* flowers, I found very small scales between the two transverse floral prophylls and the androecium (Figs. 9, 10). That they are different from the "metaxyphylls" below the terminal flowers and more intimately connected with the flower is shown by the following features: (1) they are smaller and nearer to the androecium than the metaxyphylls, (2) there is a temporal gap between the early appearing two lateral prophylls (however reduced they are) and the additional scales, and (3) if the scales would correspond to the metaxyphylls one would expect the highest number in the lowermost lateral flower (which has, at times, secondary lateral flowers). In the inflorescence shown in Figures 14–19 the reverse is the case: the lowermost lateral flower (Fig. 18) does not even have a single scale on the abaxial side, whereas an upper lateral flower (Fig. 19) shows a scale.

In the material examined, the number (and apparently also the position) of these scales varies from zero to five. In contrast to the tepals of *Tetracentron,* these scales do not protect the floral organs in any phase of ontogeny. The protective function is provided strictly by the cataphylls and young foliage leaves of the reproductive shoot. In flowers at anthesis these scales are obscured by the general thickening of the floral base (Fig. 7).

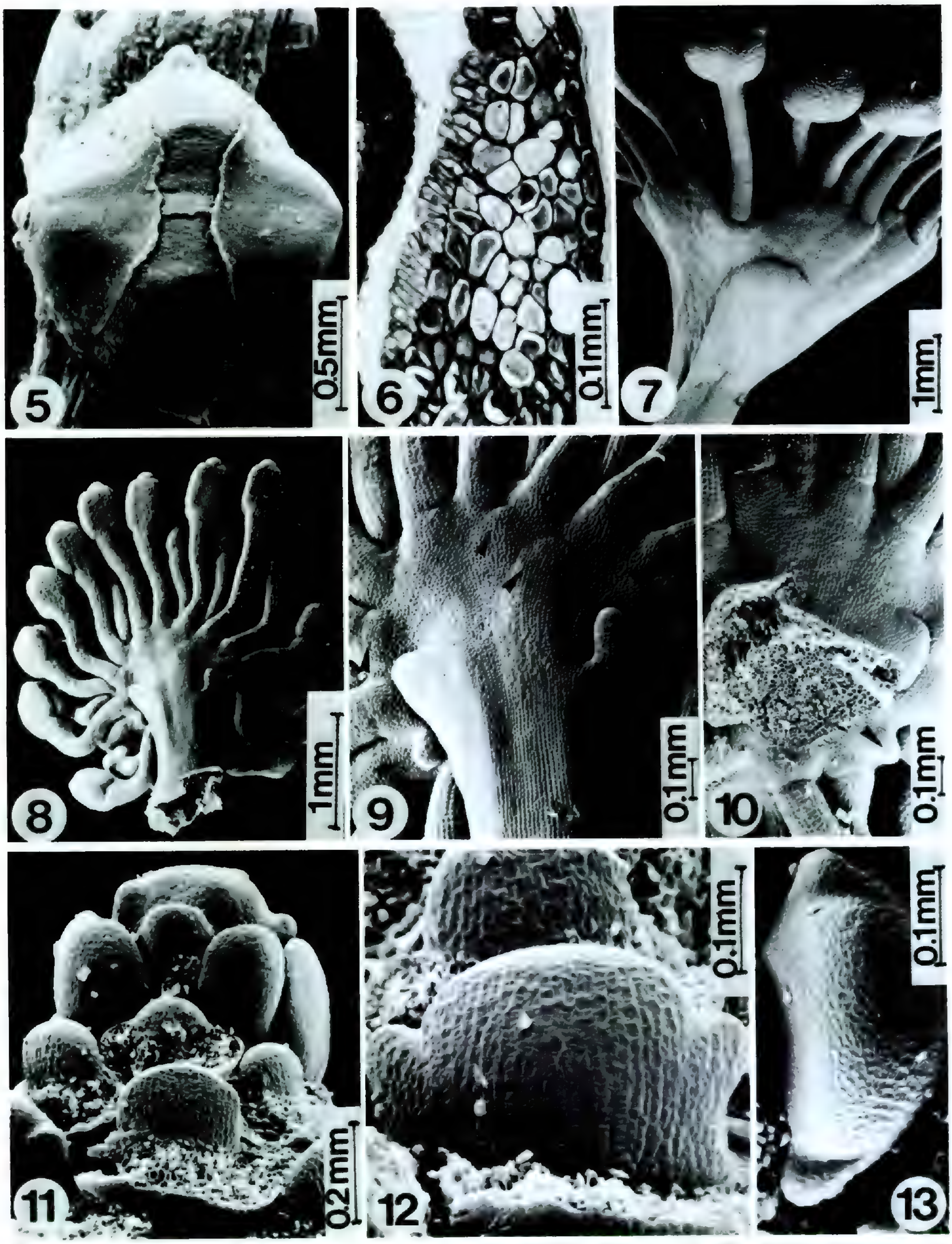
Euptelea. The inflorescences are also racemes, but the main axis of the raceme transforms into a vegetative shoot after production of the reproductive part (proliferation, Troll, 1964; auxotelic raceme, Briggs & Johnson, 1979). The flowers have no perianth (Fig. 22), but the lowermost flowers of a raceme often have one or two tiny transverse prophylls (Endress, 1969) (Figs. 20, 21). After production of the prophylls, the floral primordia of *Euptelea* and *Trochodendron* look similar in their peculiar zygomorphic or bilateral symmetry (see section on floral ontogeny). However, later, the floral axis elongates above the prophylls in *Euptelea* (Fig. 20), but below in *Trochodendron* (Fig. 12). Therefore, at anthesis, the prophylls are at the base of the pedicel in *Euptelea,* but on the top in *Trochodendron.*

Cercidiphyllum. Both perianth and floral prophylls are lacking. The inflorescences are congested spikes (heads).

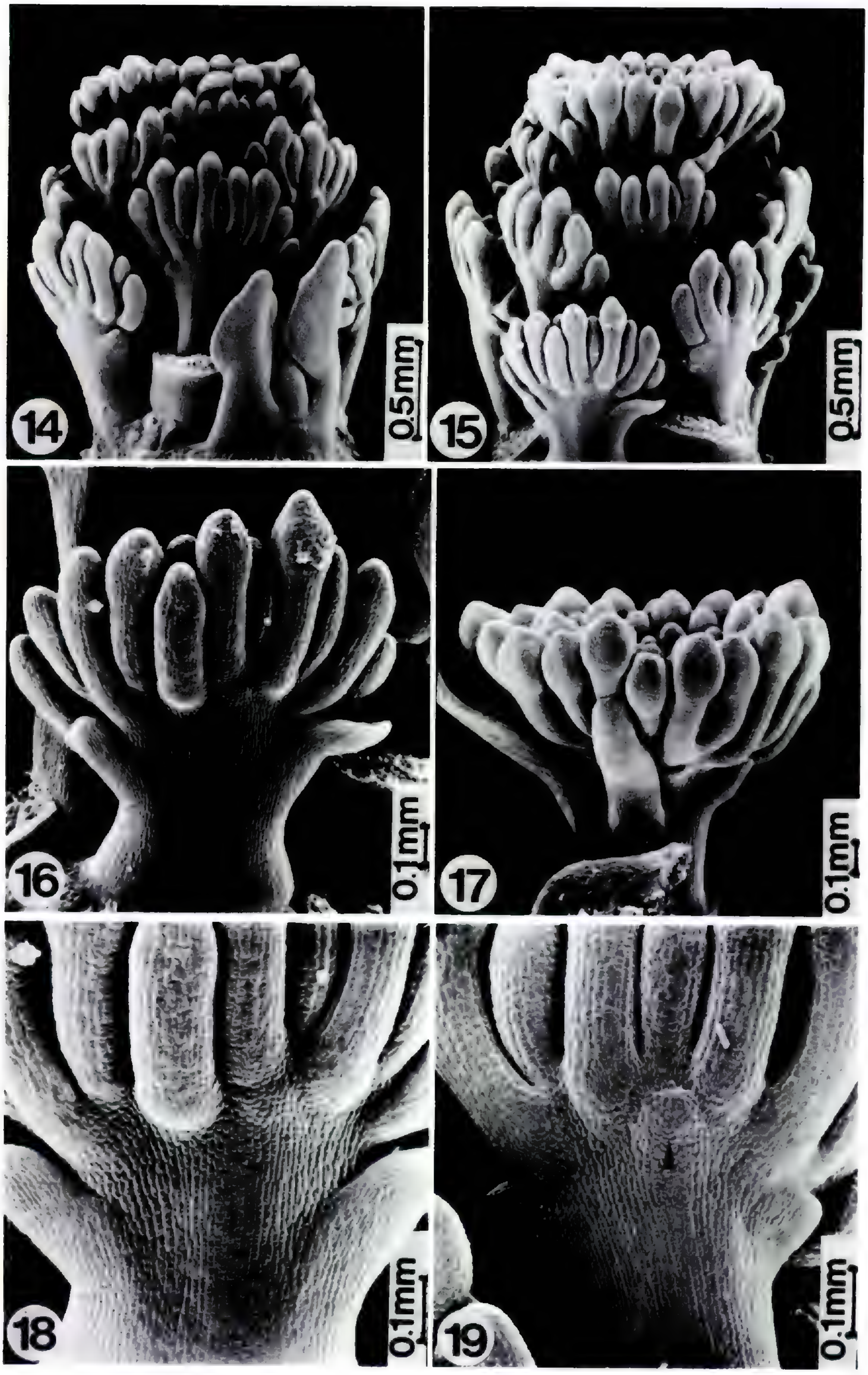
General. How do these new results influence the morphological and phylogenetic interpretation of the perianth in the Trochodendrales? The generally held view is that *Tetracentron* has a perianth of four tepals, but the other genera have naked flowers.

But if we ask instead, "How many phyllomes are between the base of the floral axis and the androecium?" the result is very different. All genera except *Cercidiphyllum* (*Euptelea* at least in some of the flowers) have a first pair of transverse phyllomes that can be called prophylls. *Tetracentron* has two more phyllomes, *Trochodendron* up to five more. In both genera they are small and not or only weakly vascularized (even in *Tetracentron,* see also Nast & Bailey, 1945). Considered this way, there is no sharp contrast between *Tetracentron* and *Trochodendron.* There is rather a gradual reduction from *Tetracentron* to *Trochodendron* and *Euptelea* to *Cercidiphyllum* (Fig. 23).

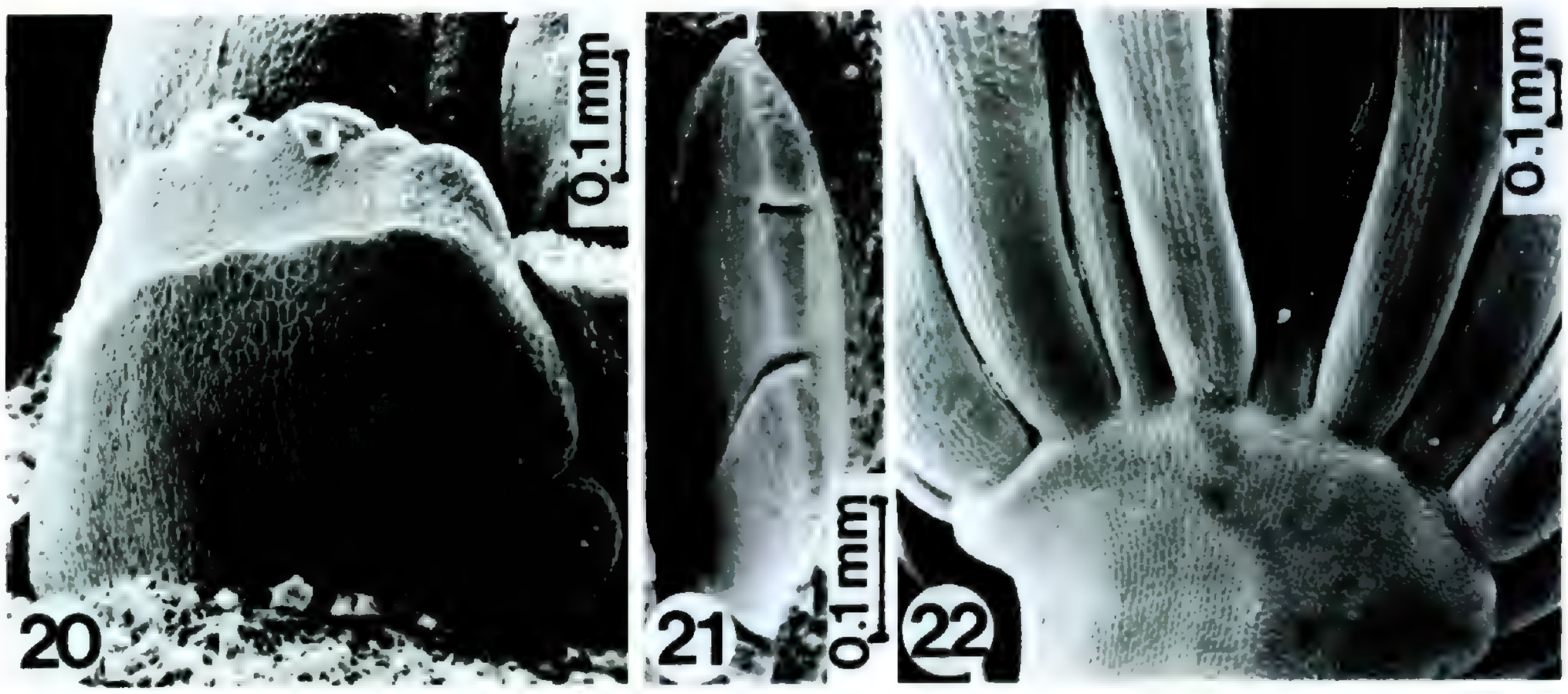
Whether these rudimentary phyllomes in *Trochodendron* should be regarded as tepals or as bracts remains somewhat ambiguous. We can state that there *are* phyllomes between prophylls and stamens, which precede the series of floral organs (sporophylls). At this evolutionary level of flowers exhibiting spiral phyllotaxis and lacking differentiation in calyx and corolla, it is always difficult to delimit a perianth from the preceding series of bracts (e.g., Endress, 1980a, 1980b, for *Austrobaileya* and *Hortonia*; Endress & Sampson, 1983, for Trimeniaceae). However, the long plastochron after formation of the two



FIGURES 5–13. 5, 6. *Tetracentron sinense*.—5. Old flower bud with pherophyll (below) and four tepals, ×30.—6. Base of tepal of flower at anthesis in longitudinal section with small-celled inner epidermis, ×140. 7–13. *Trochodendron aralioides*.—7. Base of flower at anthesis from the side, with one of the two prophylls visible, ×10.—8. Lateral flower from bud (February) from abaxial side, ×15.—9. The same, enlarged, showing the two prophylls and five rudimentary "tepals" (arrows!), ×50.—10. Lateral flower bud with the pedicel removed, showing one rudimentary tepal on adaxial side, ×50.—11. Young inflorescence (July); in lower part floral pherophylls removed to show floral primordia, ×65.—12. Floral primordium from adaxial side, with two (distal) prophylls, ×140.—13. Same, from above, to show the floral zygomorphy, ×130.



FIGURES 14–19. *Trochodendron aralioides,* young inflorescence (August).—14. Entire inflorescence from the side; on right side vegetative bud with two large prophylls, ×25.—15. Same, from the opposite side, ×25.—16. Lowermost lateral flower, with relatively large prophylls, ×55.—17. Terminal flower, after removal of all lateral flowers, to show the "metaxyphylls" (cf. page 300).—18. Same as Fig. 16, enlarged, tepal rudiments lacking, ×85.—19. Lateral flower from middle region, with smaller prophylls and one rudimentary tepal (arrow!), ×90.



FIGURES 20–22. *Euptelea polyandra.*—20. Floral primordium (July) from abaxial side, with one (basal) prophyll, ×100.—21. Younger floral primordium (July) from above, to show the bilateral (or zygomorphic) symmetry, ×110.—22. Base of old floral bud (December), rim around stamens by thickening of floral base, no tepals, ×45.

prophylls may be seen as a sign that the subsequently formed scales are to some extent integrated into the floral organization. In contrast, within the Hamamelidaceae there are obvious reduction series from flowers with well-differentiated protecting sepals in addition to petals (e.g., *Hamamelis*) through flowers with reduced and unprotective tepals (e.g., *Sycopsis*) to perianthless flowers (e.g., *Distyliopsis*) (Endress, 1977, 1978).

I conclude, based on this, that it is highly improbable that the Trochodendrales are primitively completely devoid of a perianth.

ANDROECIUM

Tetracentron and Trochodendron. The androecium is composed of four stamens in *Tetracentron,* but of a variable number of 39 to 46 for lateral flowers and around 70 for terminal flowers in *Trochodendron* (Liao, 1973: 34–57). In *Tetracentron* stamens are much smaller and stouter than in *Trochodendron.*

A newly found feature of systematic importance in both *Trochodendron* and *Tetracentron* is that each theca does not open simply by a longitudinal slit but by two valves (Figs. 24–28, 32). The longitudinal dehiscence line extends into two transversal lines at both ends, which results in two window wing-like valves. This feature underlines at the same time the close relationship between *Tetracentron* and *Trochodendron* and their affinities with Hamamelidales (Fig. 32), especially since this feature is otherwise very rare in the angiosperms. Although "valvate" anthers have been mentioned in the literature for various higher groups of the angiosperms, it seems that most taxa actually have simple longitudinal slits without transverse extensions. At present, real valvate anthers seem to be restricted to a few Magnoliidae (Laurales) and Hamamelidae (Fig. 32), whereby those of the Laurales are of a slightly different type. However, the search has to be extended to other angiosperms. Further similarity with Hamamelidales is provided by the ba-

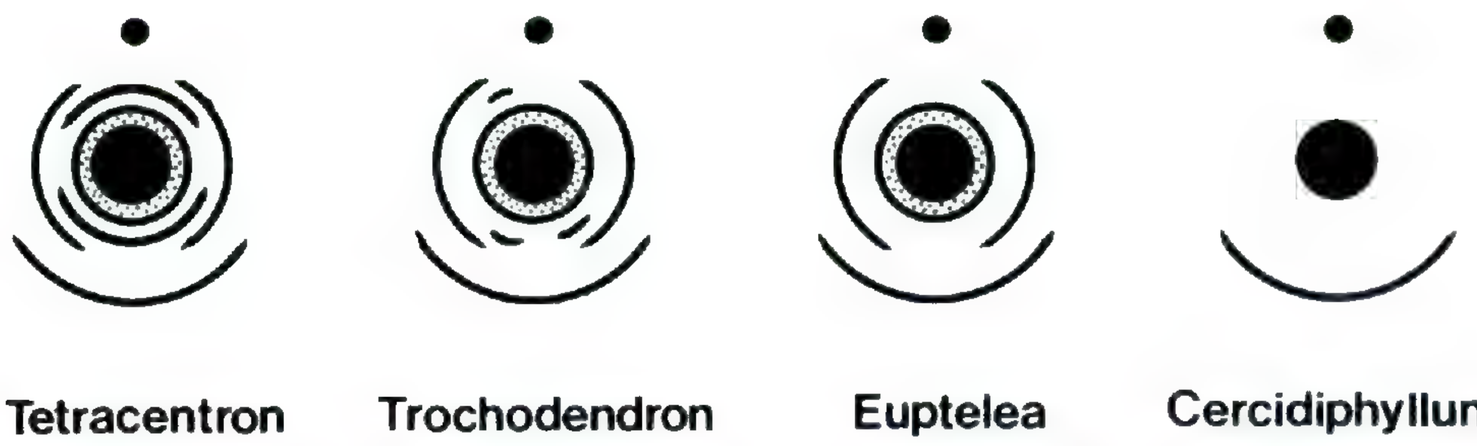
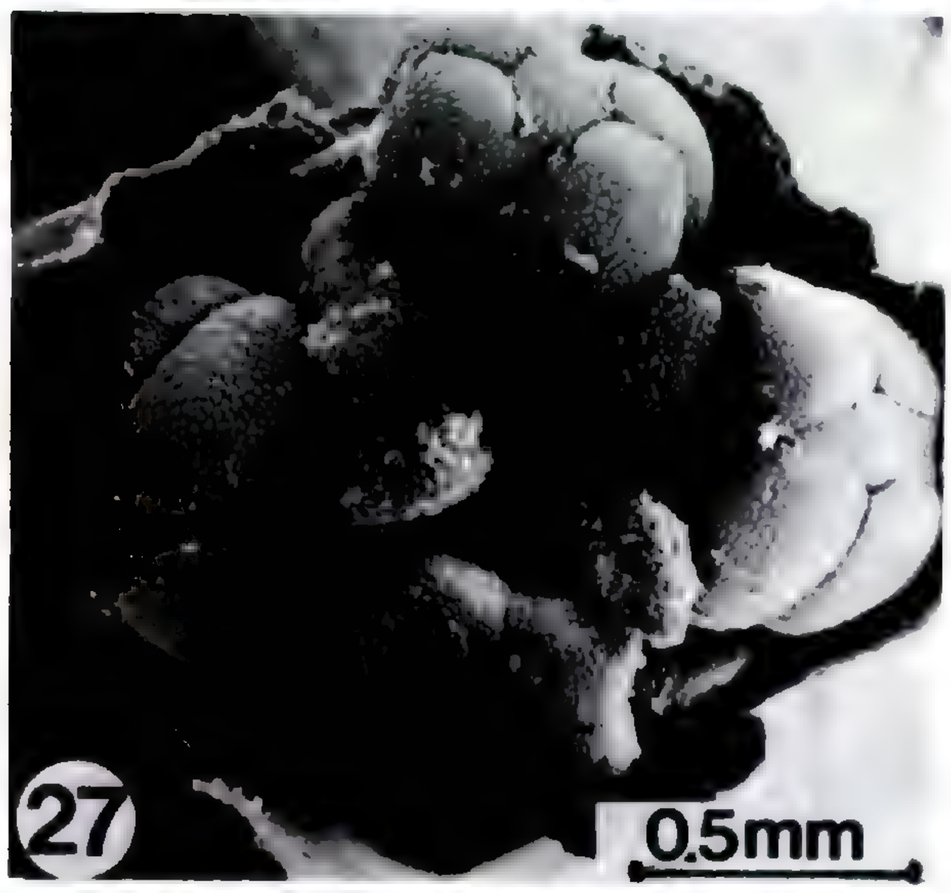
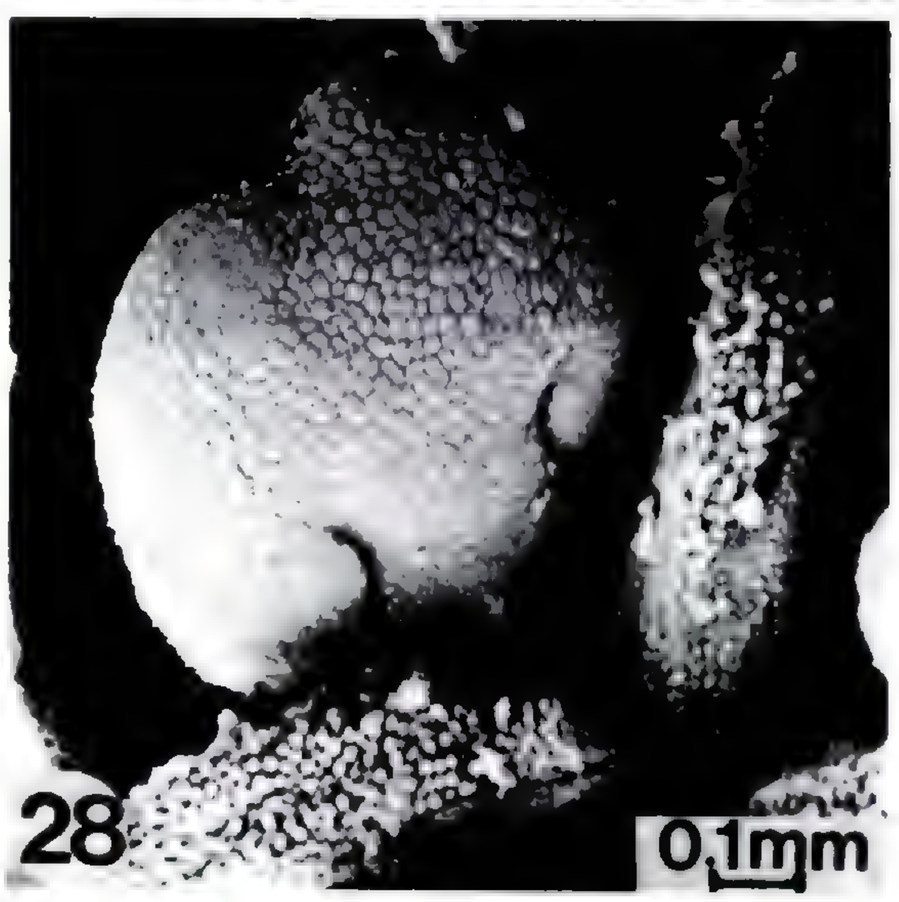
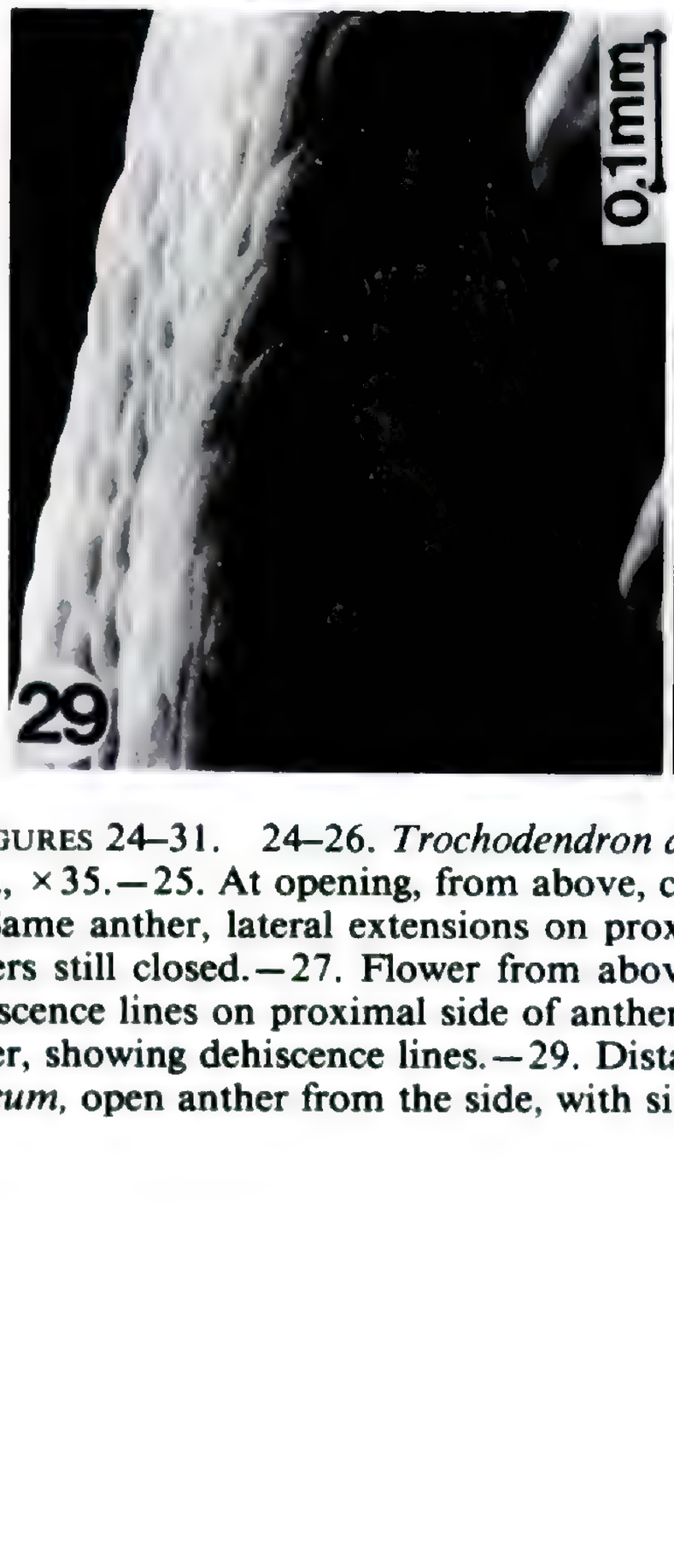
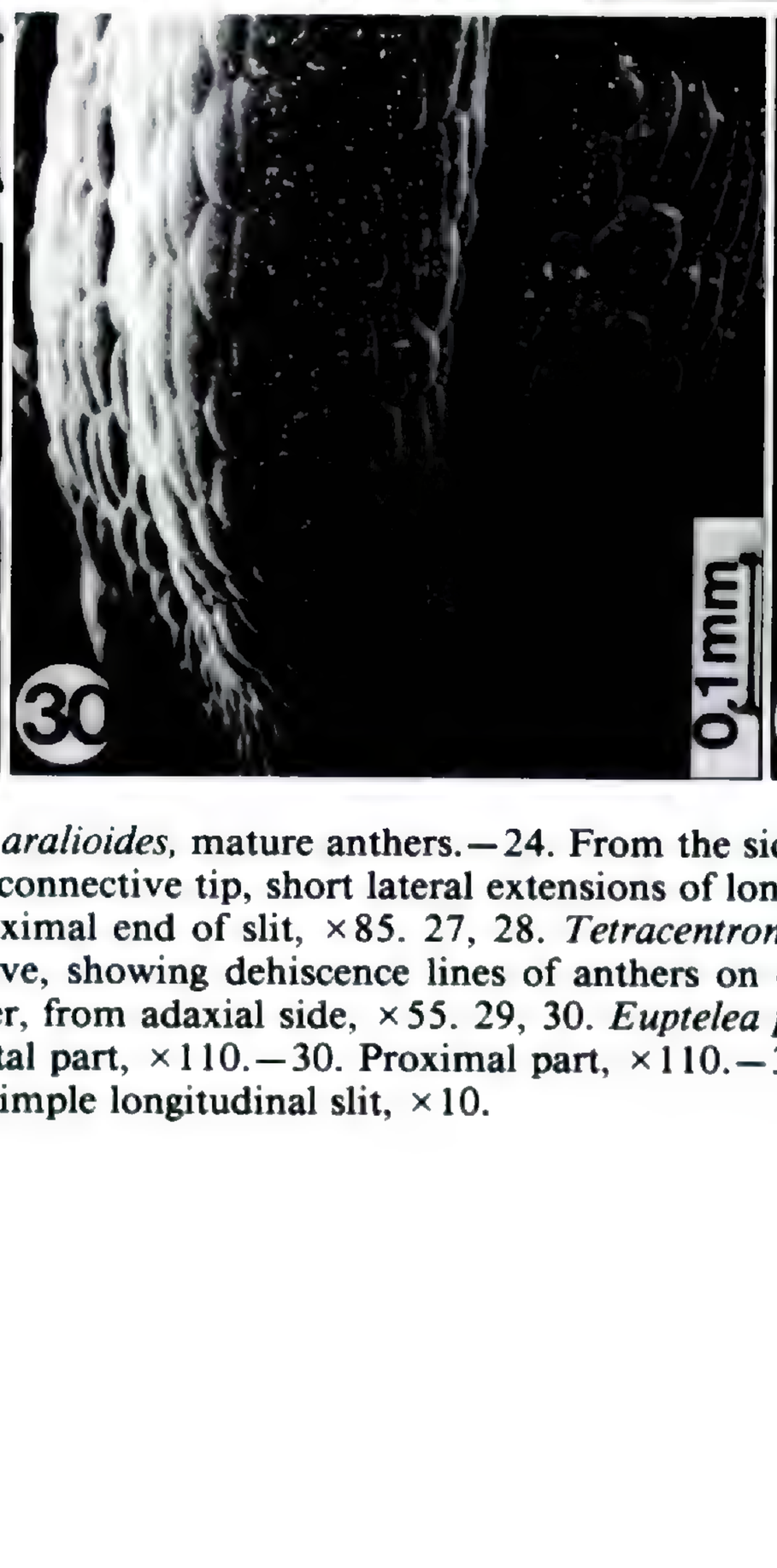


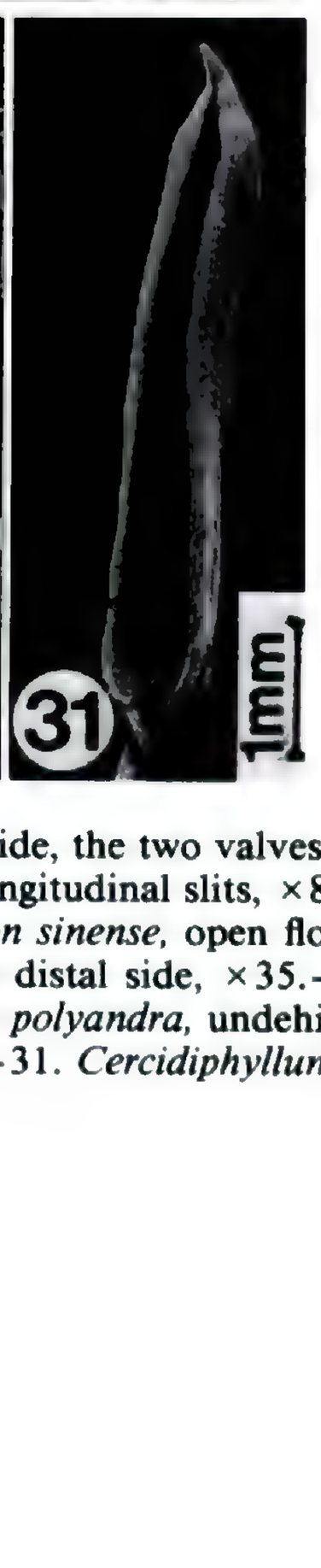
FIGURE 23. Floral diagrams showing floral pherophylls (6:00 position), prophylls (3:00 and 9:00), and tepals. Androecium (stippled) and gynoecium (black) not differentiated. *Cercidiphyllum*: diagram for female flower only.











FIGURES 24–31. 24–26. *Trochodendron aralioides,* mature anthers.—24. From the side, the two valves of a theca, ×35.—25. At opening, from above, connective tip, short lateral extensions of longitudinal slits, ×85.—26. Same anther, lateral extensions on proximal end of slit, ×85. 27, 28. *Tetracentron sinense,* open flower, anthers still closed.—27. Flower from above, showing dehiscence lines of anthers on distal side, ×35.—28. Dehiscence lines on proximal side of anther, from adaxial side, ×55. 29, 30. *Euptelea polyandra,* undehisced anther, showing dehiscence lines.—29. Distal part, ×110.—30. Proximal part, ×110.—31. *Cercidiphyllum japonicum,* open anther from the side, with simple longitudinal slit, ×10.

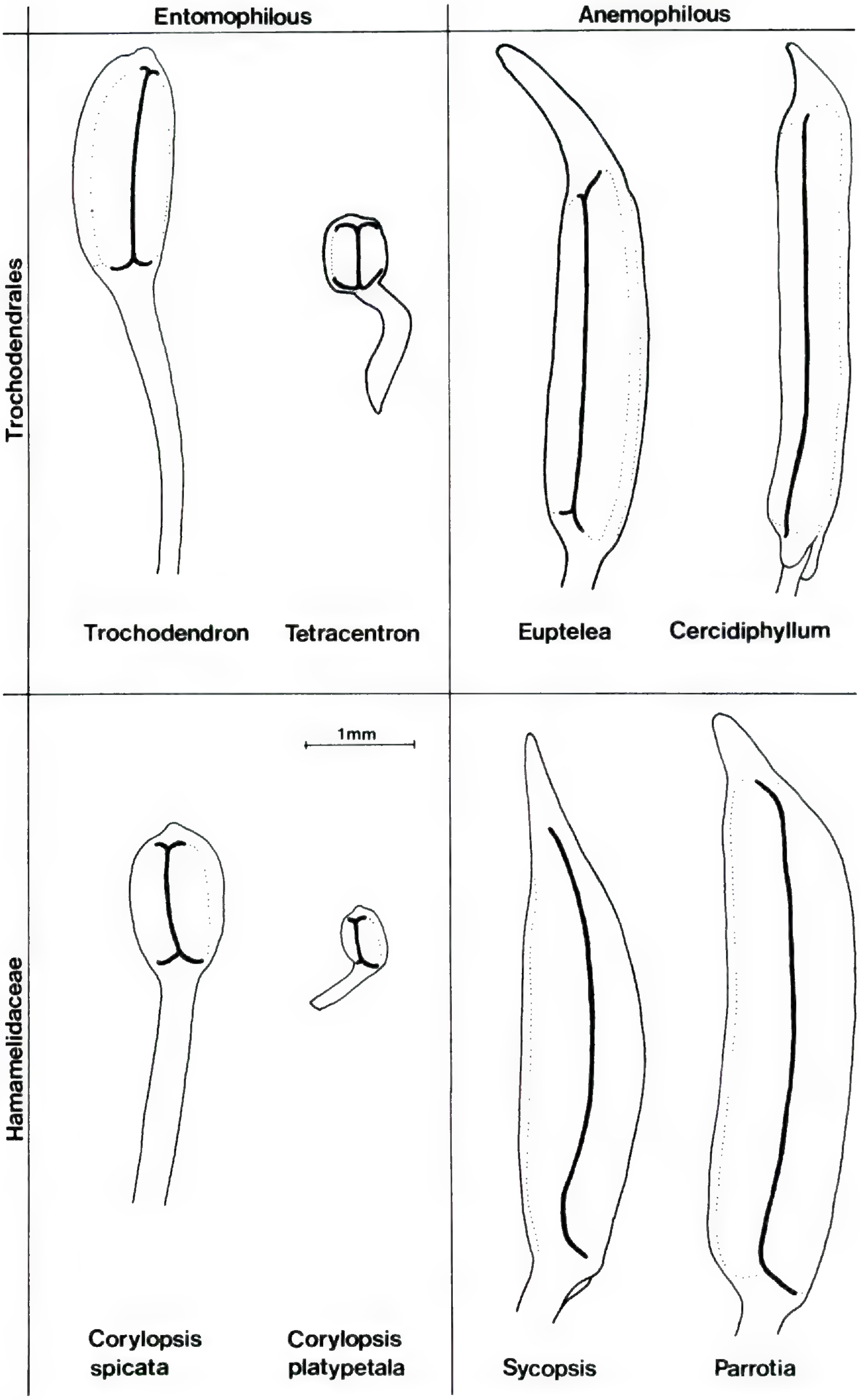


FIGURE 32. Similarity and parallel variation of anther shape, size and dehiscence in correlation with entomo- and anemophily in Trochodendrales and Hamamelidaceae. All stamens from the side, adaxial side left. (*Corylopsis spicata, C. platypetala, Sycopsis sinensis,* and *Parrotia persica,* all from cultivated material, old Botanical Garden, University of Zürich).

sifixed, more or less latrorse anthers with a rudimentary connective tip (Fig. 32).

Euptelea and Cercidiphyllum. In both genera the stamen number is variable: *Euptelea* with six to 19 per flower (Endress, 1969) and *Cercidiphyllum* with at least seven in the lowermost flowers. As part of the anemophily syndrome, the anthers are long and contain more pollen than in *Tetracentron* and *Trochodendron.* In *Cercidiphyllum* they open by simple longitudinal slits (Figs. 31, 32). However, in *Euptelea,* there are very short horizontal extensions of the dehiscence line, mainly at its lower end, which results in two narrow valves on each theca (Figs. 29, 30, 32). As in *Trochodendron* and *Tetracentron,* the anthers are basifixed, more or less latrorse, and provided with a connective tip. The connective tip, however, is longer in *Euptelea* and *Cercidiphyllum* than in *Trochodendron* and *Tetracentron* (Fig. 32), presumably as a result of the early longitudinal growth of the entire anther.

General. It is striking that the range of anther shape in the four genera of Trochodendrales is repeated in Hamamelidaceae (Fig. 32). Also in Hamamelidaceae, long anthers with mass production of pollen and dehiscence by longitudinal slits occur in predominantly wind-pollinated groups, whereas short anthers with less pollen and dehiscence by valves, on which the sticky pollen is presented, are typical for the mainly insect (often fly!)-pollinated groups (Endress, 1977).

POLLEN

In all four genera the pollen grains are triaperturate and more or less spheroidal, but in *Euptelea* also often pluriaperturate (Praglowski, 1974; Walker, 1976a, 1976b). The apertures are well delimited and coarsely granulate.

Trochodendron and Tetracentron. In pollen structure the two genera are again strikingly similar, also in details not previously mentioned in the literature. Both are tricolpate. The tectum consists of distinct rods that are irregularly interwoven and form a loose network between the apertures but are crowded into parallel bundles along the aperture borders (Figs. 33, 34, 37). In short, the exine is rugulate-reticulate between the apertures but striate near the apertures in both genera. In both genera, especially in *Tetracentron,* the pollen is very small (10–15 μm diam.). On the whole, the similarity in exine structure between the two genera is even more accentuated than stated by Praglowski (1974) and Walker (1976a, 1976b).

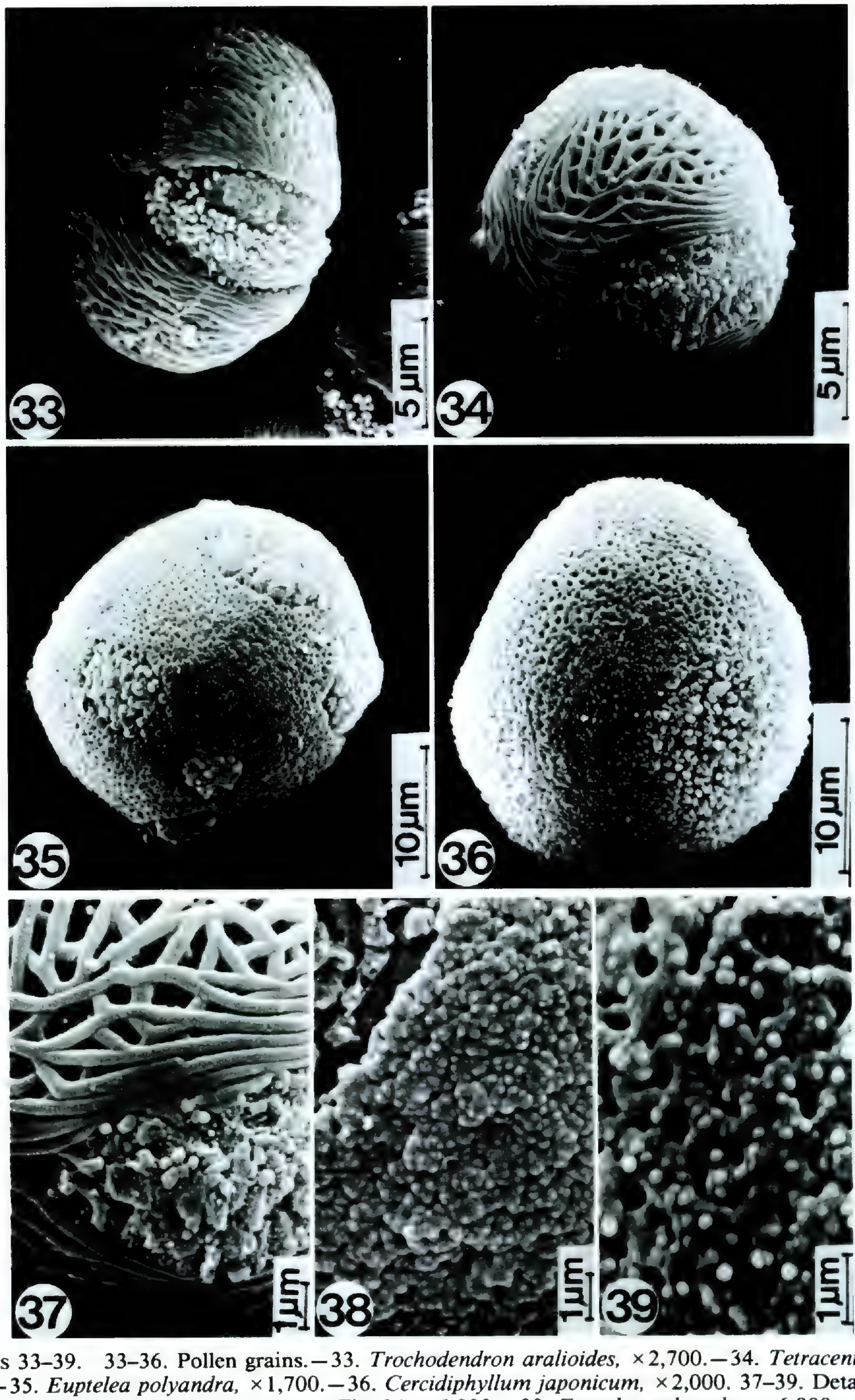
Euptelea and Cercidiphyllum. In both genera the exine is finely reticulate, with minute tectal perforations, and scabrate (with supratectal verrucae). The apertures are shorter, more roundish in outline than in *Trochodendron* and *Tetracentron* (Figs. 35, 36, 38, 39). In both *Euptelea* and *Cercidiphyllum,* the apertural exine is coarsely structured. *Euptelea* pollen often has more than three apertures, in contrast to *Cercidiphyllum.* In both genera the pollen is considerably larger (20–30 μm diam.) than in *Trochodendron* and *Tetracentron* and fits in the normal range of wind-dispersed pollen (cf. Whitehead, 1969).

Again, the parallel between the pollen of *Euptelea* and *Cercidiphyllum* and the anemophilous genera of the Hamamelidaceae is striking in the trend to shorter apertures and more than three apertures, finer reticulation of the extra-apertural exine, and supratectal verrucae (Endress, 1977; Bogle & Philbrick, 1980).

GYNOECIUM AND NECTARY

Trochodendron. Leinfellner (1969b) gave a brief survey of the gynoecial morphology of Magnoliales, Laurales, and Trochodendrales. The elaborate diagram of a gynoecium of *Trochodendron* in Nast and Bailey (1945) does not show all the basic gross morphological features. The extension of the inner and outer surface in some critical regions remains unclear.

In *Trochodendron* the carpel number of the gynoecium varies around eight in lateral flowers and around ten in terminal flowers. Smith (1945) found a range of (4–)6–11, Liao (1973) a range of 7–11, and Cronquist (1981) a range of 4–11 (–17). In the stylar region the carpels are free and slightly recurved (Figs. 1, 40, 41a–c, 45). In the ovary, the carpel flanks are congenitally fused (Fig. 41e–i). Above the ovary there is a short zone where the neighboring, contiguous carpels are postgenitally fused (Fig. 41d). The ovary is partially inferior (Fig. 40). In the upper part of the ovary a compitum is formed by postgenital fusion of the carpels in the center, while in the lower portion of the ovary the carpels do not meet in the center, but form a ring around a central hole (Figs. 40, 41e–g). The compitum, however, is rather diffuse, because the ventral slits that are lined with a pollen tube transmitting epidermis are very long in horizontal extension.



FIGURES 33–39. 33–36. Pollen grains.—33. *Trochodendron aralioides,* ×2,700.—34. *Tetracentron sinense,* ×3,000.—35. *Euptelea polyandra,* ×1,700.—36. *Cercidiphyllum japonicum,* ×2,000. 37–39. Details of pollen surface.—37. *Tetracentron sinense,* same as Fig. 34, ×6,000.—38. *Euptelea polyandra,* ×6,000.—39. *Cercidiphyllum japonicum,* ×9,000.

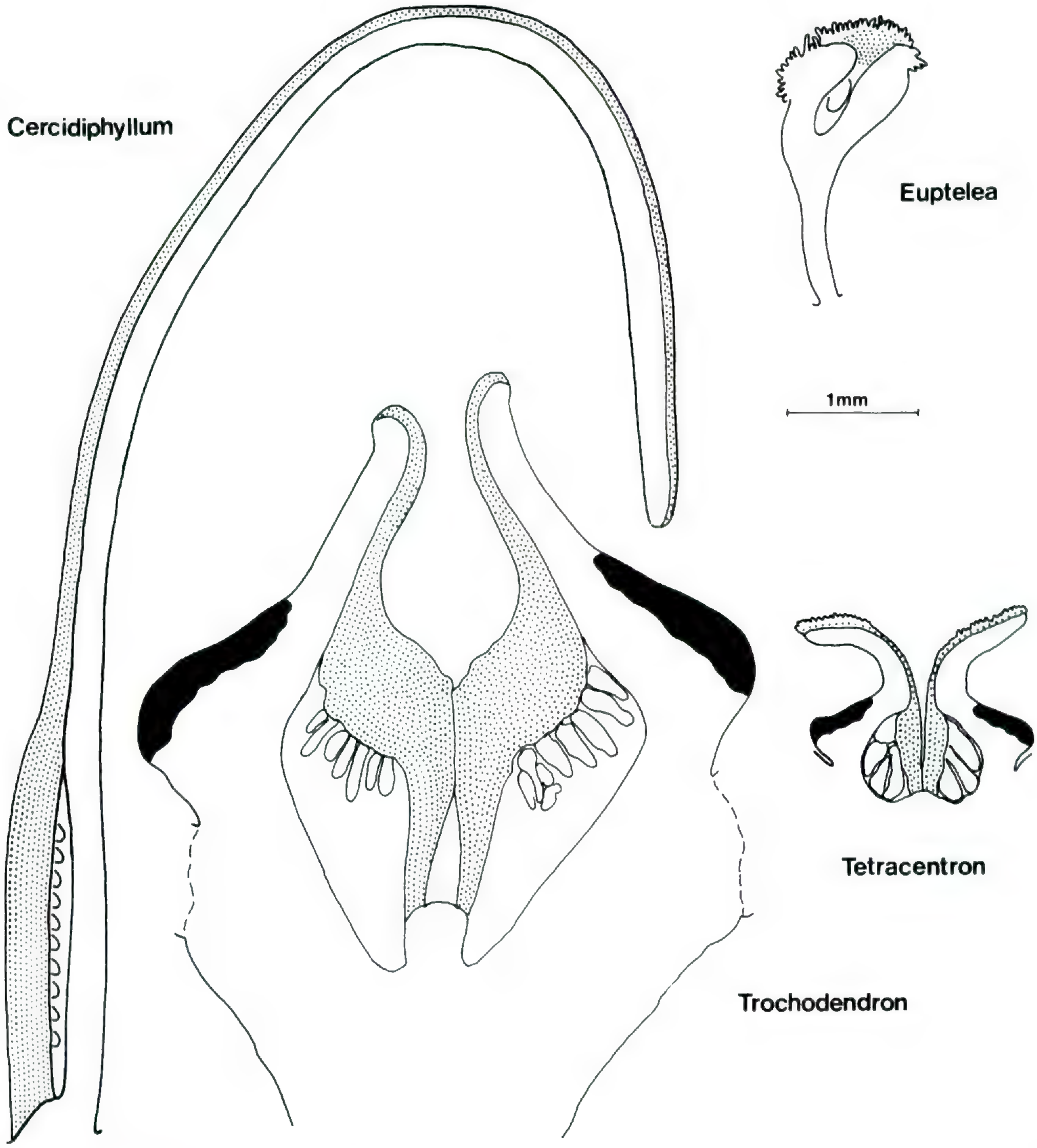


FIGURE 40. Median longitudinal sections of carpels, with ventral side on the left (*Cercidiphyllum, Euptelea*), and gynoecia (*Trochodendron, Tetracentron*) at anthesis, with outer and inner morphological surfaces (stippled, region of postgenital fusion; black, nectariferous region).

The compitum is, therefore, not as elaborated as the centralized types in the higher advanced angiosperm groups (Carr & Carr, 1961). Again, the similarity with the Hamamelidaceae is obvious (cf. Endress, 1967).

The stigmatic epidermis differentiates unicellular papillae of a dry type (category DPU in the classification of Heslop-Harrison, 1981) (Fig. 46).

Ontogenetically, the hole in the center of the gynoecium base arises because the fairly high number of carpels is arranged more or less in a whorl and therefore leaves a free field in the center of the floral apex. Gynoecial development is slow and retarded compared with that of the androecium. In mid-September, when the outer stamens were morphologically already well differentiated, the carpels were still shallow, hippocrepiform mounds (Figs. 56, 57). In mid-February, the postgenital fusion within and between the carpels had not yet started.

The carpels have a conspicuous dorsal bulge. This bulge is differentiated as a nectary (see Tieghem, 1900!) (Figs. 1, 40, 45, 50) and is vascularized by numerous phloic strands that are connected with the dorsal carpellary bundles (Nast & Bailey, 1945; Pervukhina, 1962) (Fig.

41d, e). It forms an open landing platform exposed to visitors. The epidermis of the nectary is covered with numerous slightly sunken stomata. Each stoma is surrounded by a ring of several epidermal cells with conspicuous cuticular folds (Figs. 52, 54).

All or part of the 15–30 ovules (15–20, my data; 15–28, Liao, 1973; 25–30, Cronquist, 1981) in each carpel develop into many small dust-like seeds, suited for wind-dispersal. They are released from capsules that open by ventral and short dorsal slits. The mature ovules have long integuments and a chalazal protrusion, which both contribute to seed appendages. In the chalazal appendage the ovular vascular bundle forms a hair-pin loop (Nast & Bailey, 1945; Mohana Rao, 1983). The testa differentiates five cell layers, the middle layer being sclerified (Melikian, 1973).

Tetracentron. The gynoecium of *Tetracentron* although strikingly similar to that of *Trochodendron* (Fig. 40), differs in that it is much smaller and contains only four carpels (Figs. 42c, 51), each with five or six ovules. The very similar differentiation of a nectary should be especially emphasized, since it has not been reported previously, although its presence was mentioned by Cronquist (1981). The numerous stomata on the dorsal carpellary bulges are also slightly sunken below the general surface (by the smaller size of the guard cells compared with the other epidermis cells) and surrounded by a ring of epidermal cells with prominent cuticular folds (Figs. 53, 55). Striking are also the facts that in both genera the stigma is presumably dry and has unicellular papillae (Fig. 47), that the ovary is syncarpous and semi-inferior (Fig. 40), that the ovary locules are filled with copious secretion around the ovules, and that dust-like seeds (testa five-layered with middle layer sclerified, Melikian, 1973) with a chalazal and micropylar appendage are released from small capsules. The ovules with the long integuments and chalazal protrusion with a hair-pin-like vascular bundle are very similar (Nast & Bailey, 1945) in *Tetracentron* and *Trochodendron.* Also in both genera the carpels have five main vascular bundles, three dorsal ones and one lateral one on each side (Fig. 42). *Trochodendron* has more secondary lateral veins appropriate to its larger size. In *Tetracentron* the nectary does not have a separate vascular supply, probably due to the much smaller size of the gynoecium (Fig. 42b, c).

Cercidiphyllum. The female flower consists of nothing more than a slightly stipitate single carpel on a rudimentary floral axis (Fig. 4a) (Solereder, 1899). The carpel is plicate throughout (in the terminology of Leinfellner, 1950) without any ascidiate basal portion (Fig. 43). Leinfellner's (1969b) observation of a slight indication of an ascidiate base in *Cercidiphyllum* could not be confirmed with my material (Fig. 43k). The ovary contains about 17–24 lateral ovules in two rows (17–20, my data; 20–24, Harms, 1916). The ovary is relatively small at the time of pollination and the ovules immature, and the stigma occupies about a third of the length of the carpel (Fig. 4a); it is extended over almost the entire circumference of the carpel apically and tapers towards the base (Figs. 4a, 43a, b). The stigmatic surface bears unicellular papillae and is of a dry type (Fig. 49). The carpel has three main vascular bundles (Fig. 43), a median and two laterals with a network of secondary lateral bundles in between, which are only weakly differentiated at anthesis.

The seeds have a conspicuous micropylar and a chalazal appendage with a vascular bundle describing a hair-pin loop. However, the integuments protrude less over the micropyle than in *Trochodendron* and *Tetracentron* (Swamy & Bailey, 1949).

Euptelea. The gynoecium consists of about eight to 31 free carpels (Smith, 1946; Leinfellner, 1969a; Endress, 1969). The carpels are conspicuously stipitate, but lack a style. The ovary is strongly ascidiate (Fig. 44) and contains 1–3(–4) lateral ovules that are, as in *Cercidiphyllum,* immature at anthesis. The stigmatic surface sits immediately on the ovary; it bears long, unicellular papillae and is of a dry type (Fig. 48). In the carpel three vascular bundles differentiate (Fig. 44), a (dorsal) median and two laterals. The two laterals fuse in the ascidiate region in proximal direction and the resulting ventral median bundle fuses with the dorsal median in the stipe (Fig. 44; Leinfellner 1969a). The carpel shape of *Euptelea* is very distinctive and resembles certain Magnoliidae, such as Winteraceae, Schisandraceae, and Ranunculaceae, much more than any Hamamelidae.

FLORAL ONTOGENY, PHYLLOTAXIS, AND FLORAL SYMMETRY

Floral symmetry and phyllotaxis are intimately correlated, at least in early developmental stages. Examples were recently shown by Tucker (1984). It seems that there is also a connection between the early floral symmetry and the ar-

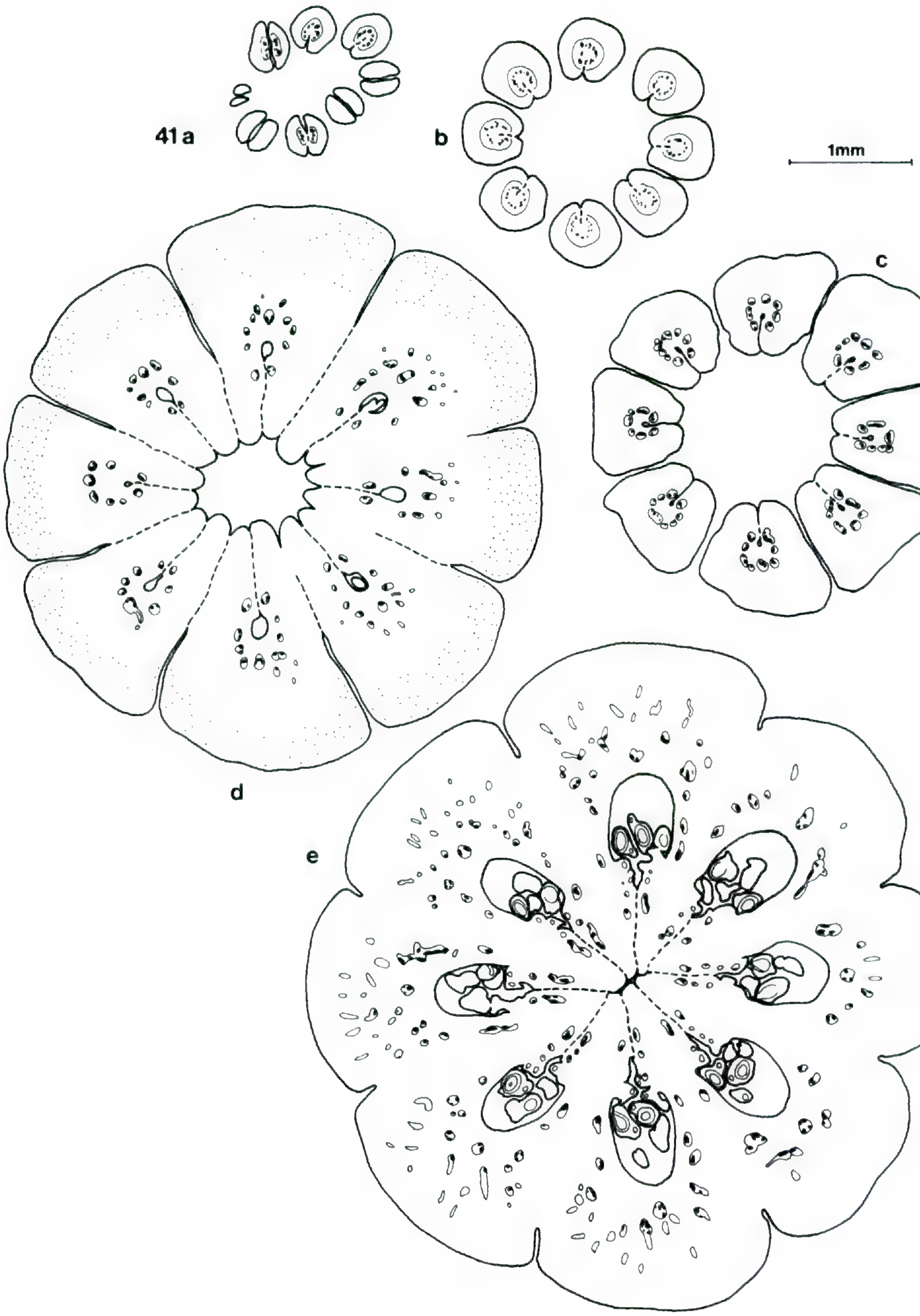
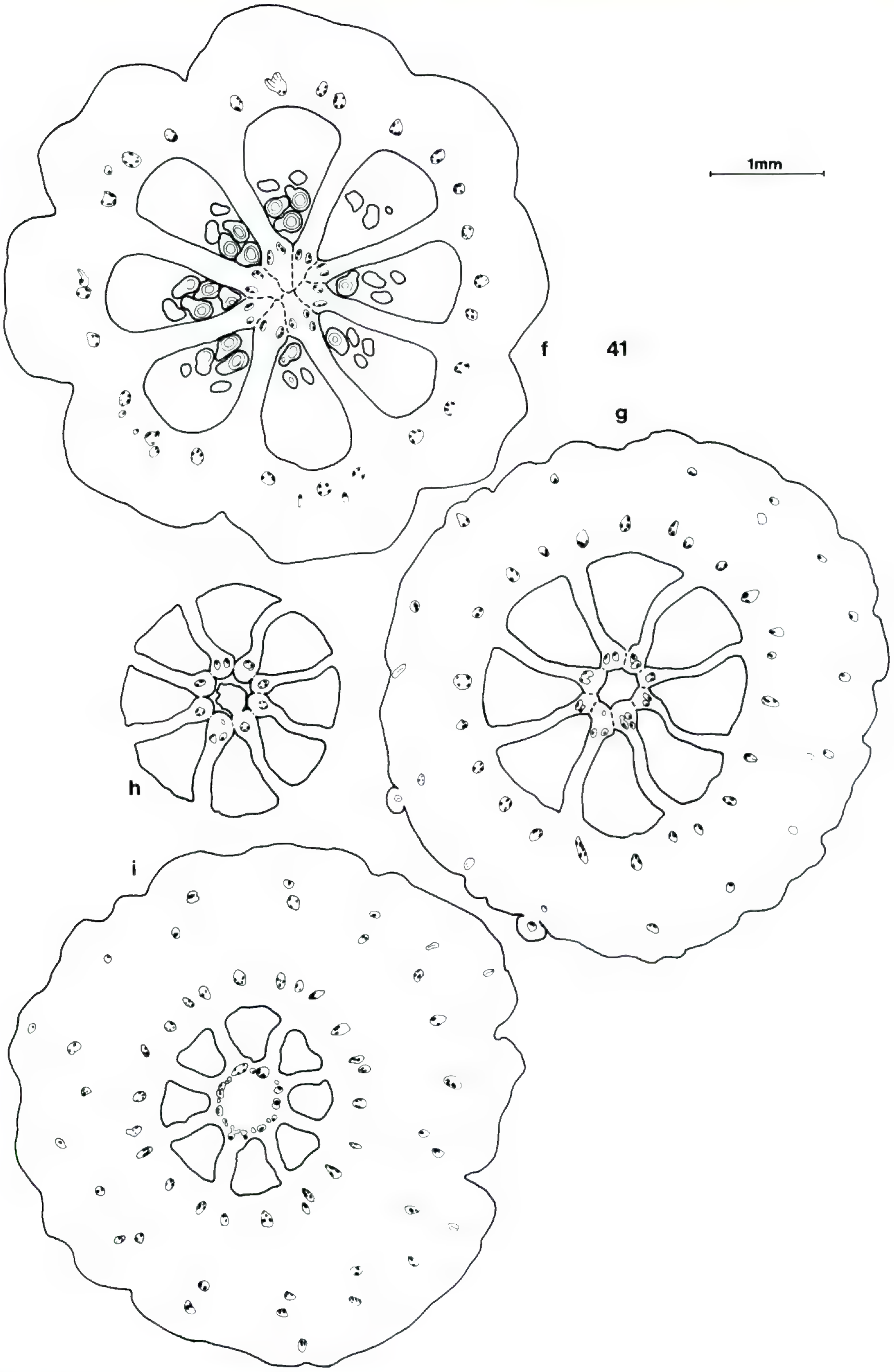


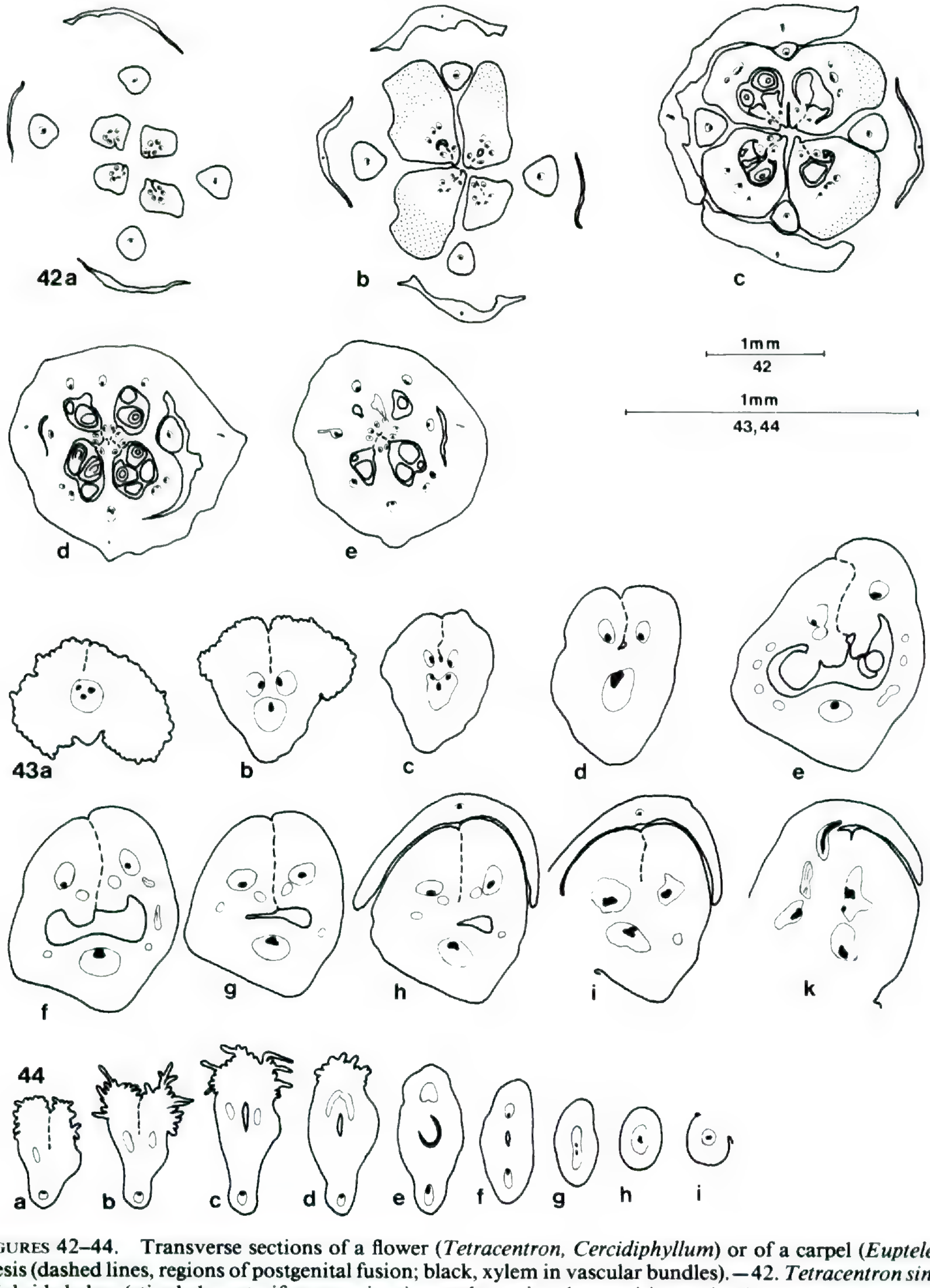
FIGURE 41a–e. *Trochodendron aralioides*. Series of transverse sections of gynoecium at anthesis (dashed lines, regions of postgenital fusion; black, xylem in vascular bundles).—a. Stigmatic region.—b. Upper stylar region.—c. Lower stylar region.—d. Transition region between style and ovary (stippled, nectariferous tissue).—e. Upper symplicate region of ovary where the carpellary flanks meet in the center; note numerous peripheral phloic bundles supplying nectaries.

→

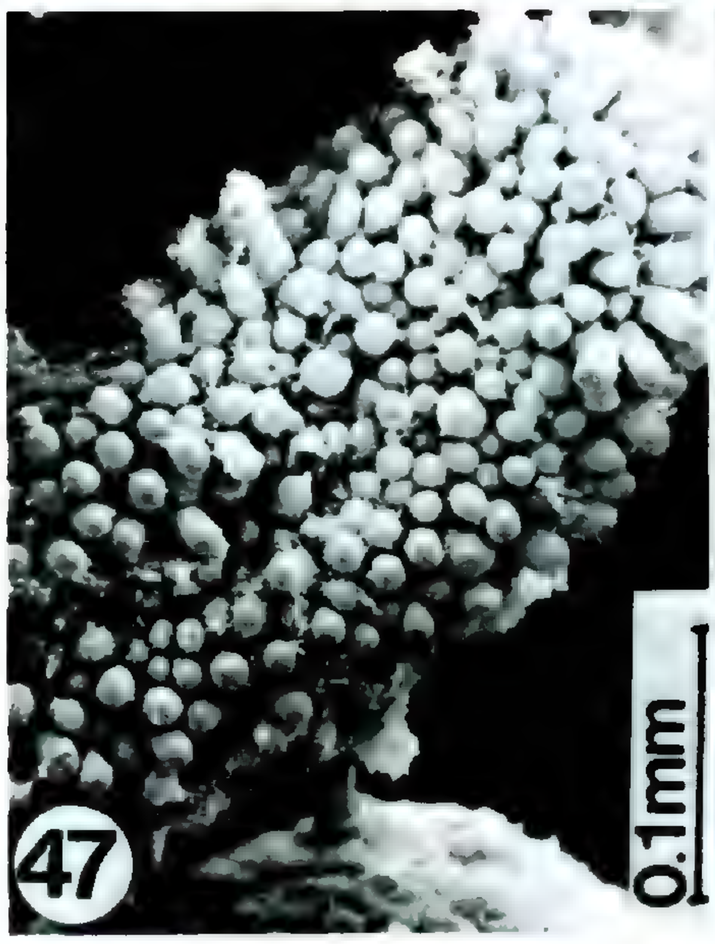
FIGURE 41f–i. *Trochodendron aralioides*. Series of transverse sections of gynoecium at anthesis (dashed lines, regions of postgenital fusion; black, xylem in vascular bundles).—f. Middle symplicate region of ovary with



minimal extension of postgenitally fused region of carpellary flanks meeting in the center (compitum).—g. Lower symplicate region of ovary with carpellary flanks retracted from the center, leaving a hole; at the periphery stamen bases and stamen traces appear.—h. Transition region between symplicate and synascidiate region (only center of ovary drawn).—i. Synascidiate region of ovary.



FIGURES 42–44. Transverse sections of a flower (*Tetracentron, Cercidiphyllum*) or of a carpel (*Euptelea*) at anthesis (dashed lines, regions of postgenital fusion; black, xylem in vascular bundles).—42. *Tetracentron sinense,* abaxial side below (stippled, nectariferous regions): a, stylar region; b, transition region between styles and ovary; c, transition region between apocarpous and symplicate region; d, symplicate region, the two median stamens fused with floral base, the two lateral stamens (partially) free; e, transition region between symplicate and synascidiate region.—43. *Cercidiphyllum japonicum,* floral pherophyll and ventral side of carpel facing upwards (in h–k): a, b, upper (a) and lower (b) stigmatic regions (wavy outline, receptive surface); c, middle stylar region; d, transition region between style and ovary; e, ovary; f, ovary below placentar region; g, ovary base; h, transition region between ovary and carpellary base; i, massive carpellary base, ventral slit (by dashed line) still present; k, carpellary base united with floral pherophyll on left side, lowermost extension of ventral slit still present.—44. *Euptelea polyandra,* ventral side of carpel facing upwards: a, b, plicate apex of carpel; c, upper ascidiate part of carpel; d, lower end of stigma, lateral bundles fusing into ventral median bundle; e, ovary with lateral ovule; f, lower end of ovary locule; g, h, carpellary base, ventral and dorsal median bundle fusing; i, carpellary base partially united with floral base.



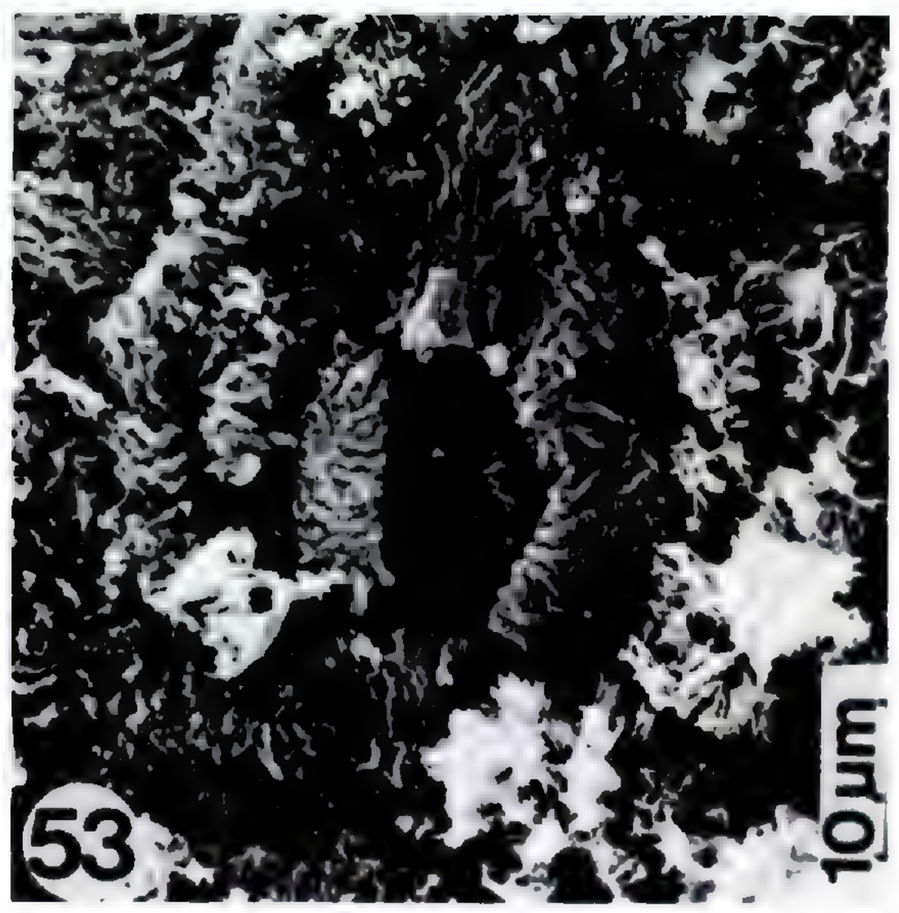
FIGURES 45–49.—45. *Trochodendron aralioides*. Gynoecium at early anthesis, ×10. 46–49. Stigmatic surfaces at anthesis.—46. *Trochodendron aralioides*, ×120.—47. *Tetracentron sinense*, ×170.—48. *Euptelea polyandra*, ×30.—49. *Cercidiphyllum japonicum*, ×130.

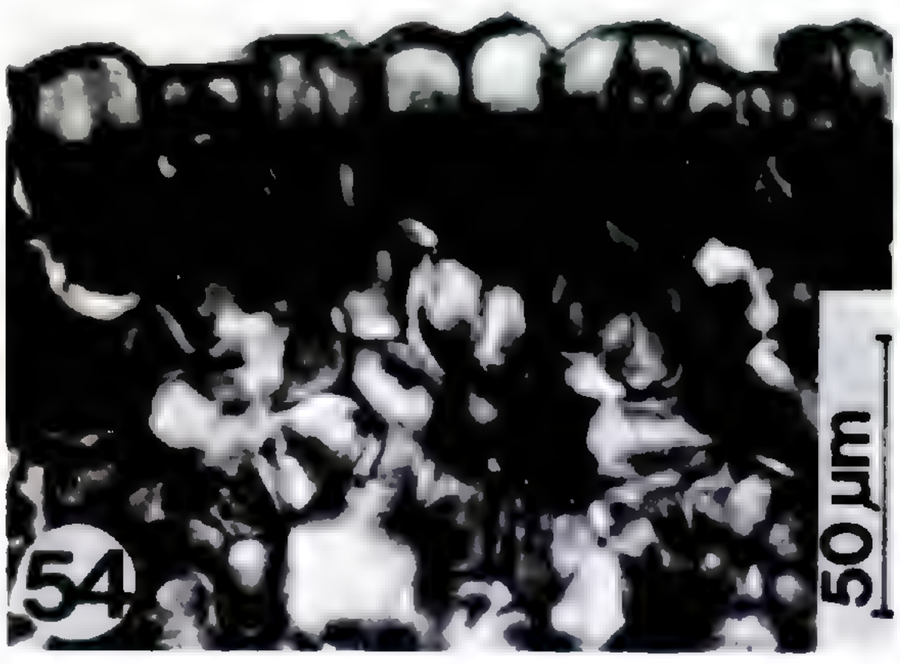
chitecture of the entire shoot bud (Endress, 1969), which is obvious in *Trochodendron, Euptelea,* and *Cercidiphyllum.*

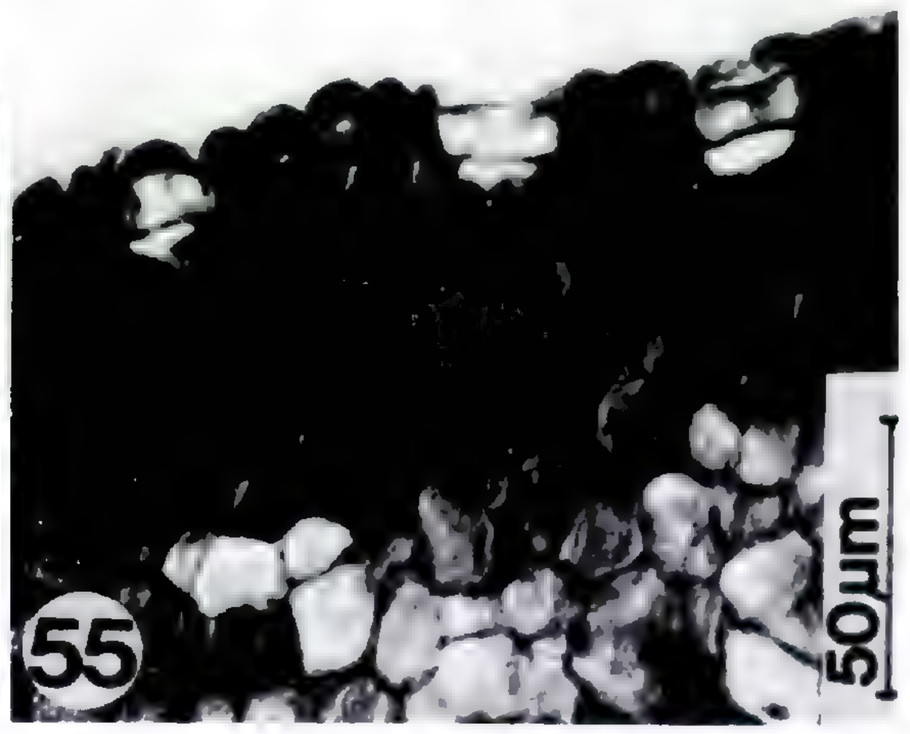
Trochodendron. The young flowers have been shown to pass through a zygomorphic phase with a conspicuous *ad*axial growth retardation of stamen primordia, although at anthesis they have (re)gained a radial symmetry (Pervukhina & Yoffe, 1962). However, this is only true for the lateral flowers of the inflorescence (Fig. 56), and the terminal flower is radial throughout its ontogeny (Fig. 57).

The androecium has usually been described as being spirally arranged. This seems to be true from the earliest ontogenetic stages and it can be extended to the gynoecium. This is even implied by the frequent occurrence of eight carpels, which is a Fibonacci number. As in *Illicium* (Robertson & Tucker, 1979), the broad residual floral apex favors a secondary more or less whorl-like arrangement of the spiral carpels. It is interesting that the spiral arrangement is also present in the lateral flowers. Therefore, it can be supposed that in the youngest stages when the stamens and carpels are initiated, the floral apex is (at least) not (strongly) zygomorphic. This problem and the exact phyllotaxis have to be studied by detailed ontogenetic investigations.

Tetracentron. The flower is described as having three tetramerous whorls, with the stamens opposite the tepals, but the carpels alternating with the stamens (Bailey & Nast, 1945). However, the flowers are more exactly described as dimerous in the perianth and androecium with four alternate pairs of organs, but tetramerous in the gynoecium (Fig. 2). The two tepal pairs are distinct by their aestivation, the two stamen pairs by the position of the anthers. Only the two me-







FIGURES 50–55. 50, 51. Gynoecium at anthesis, from above, showing nectariferous dorsal bulges of the carpels.—50. *Trochodendron aralioides,* sunken stomata visible as black dots, ×25.—51. *Tetracentron sinense,* styles removed, nectaries covered with secretion, ×30. 52, 53. Sunken stoma of nectary, encircled by several epidermal cells.—52. *Trochodendron aralioides,* ×600.—53. *Tetracentron sinense,* ×960. 54, 55. Longitudinal section of nectariferous surface with sunken stomata.—54. *Trochodendron aralioides,* ×350.—55. *Tetracentron sinense,* ×350.

dian stamens are contiguous in bud, while the two lateral ones are more remote. Further, the lateral tepals and stamens are attached at a lower level than the median ones, as seen from transverse section series (Fig. 42d). Therefore, the flowers are not exactly radial, but slightly bilaterally symmetric. Unfortunately, the early floral ontogeny is still unknown in *Tetracentron.*

Euptelea. The flower has a radial symmetry at first glance. However, the floral base is broader in transverse than in median direction, and is, therefore, bilaterally symmetric as in *Tetracentron.* Interestingly, floral primordia show a similar pattern of zygomorphy as in *Trochodendron.* However, it is just reversed in that mostly the *ab*axial side is retarded (Figs. 58, 59).

Cercidiphyllum. The female flowers are necessarily "zygomorphic," since they consist of a single carpel, which is directed towards the subtending bract (pherophyll of the flower). Leroy (1980) ascribed a special morphological significance to this position. However, it is the position that would be expected for the first phyllome of a lateral shoot with an adaxial prophyll in the same way as it occurs in the vegetative region of *Cercidiphyllum.* Ontogeny shows that not only the flowers but also the entire inflorescence is zygomorphic (Fig. 60). The inflorescence primordium is directed towards the adaxial side. The flowers appear in one or two decussate pairs. The first (transversal) pair of subtending bracts (pherophylls of the flowers) is not exactly opposite, but both are positioned somewhat towards the adaxial side. The second (median) pair of pherophylls is exactly opposite, since it is situated in the symmetry plane of the inflorescence (Fig. 60). One or both pherophylls of the second pair may be lacking, but its "carpel" is present (Fig. 61). Other authors have found up to three (to four) pairs of flowers (Swamy & Bailey, 1949; Spongberg, 1979). Van Heel (pers. comm.) observed a distinct rudimentary floral apex between the carpel and the pherophyll in another specimen.

The male flowers of *Cercidiphyllum* are difficult to delimit. The inflorescence contains about 25–32 stamens (Harms, 1916: 16–35) (Figs. 68, 69). Since the symmetry of the young inflorescence and the position of the bracts in the floral region is the same as for the female, a similar position for the flowers has to be expected: two more or less opposite flowers or several flowers in decussate pairs (Figs. 62–67). However, it is difficult to find floral boundaries. All stamens have the thecae in a lateral position relative to the inflorescence axis and all have collateral bundles or at least the xylem more towards the center of the inflorescence axis (Figs. 68, 69). From this one can judge that all turn their ventral side towards the inflorescence axis. According to this interpretation of the inflorescence, all flowers would, then, be highly zygomorphic, with stamens only on the abaxial side of the flower. In early ontogeny the median stamen of each flower would be the largest, the lateral ones successively retarded (Figs. 62, 65, 67). Thereby, the lowermost flower on the adaxial side of the inflorescence axis (frontal view in Fig. 65) would contain the highest stamen number, whereas the lowermost flower on the abaxial side (frontal view in Fig. 64), the lowermost lateral flowers (frontal view in Figs. 66, 67), and the more apical flowers of the inflorescence would contain fewer stamens.

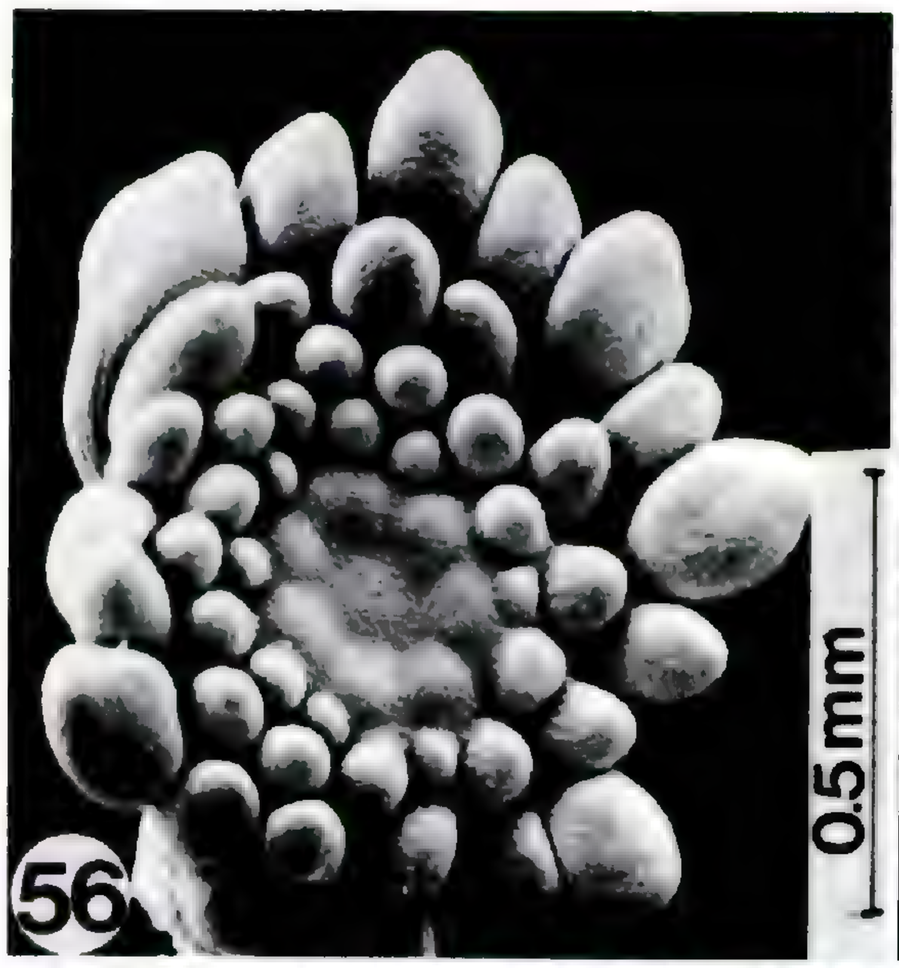
Another tentative, but perhaps less convincing, interpretation would be that the first pair of individual flowers consists of the row of about seven stamens adjoining each of the two lateral bracts. Each bract of the second (i.e., the median) pair (if present at all) has only about one to three stamens in its axil. The following stamens replace bracts in some sense and form a terminal flower (as in some Hamamelidaceae, cf. Endress, 1978; Wisniewski & Bogle, 1982). The residual apex on top of the inflorescence would be the apex of the inflorescence in the first interpretation, but the apex of the terminal flower in the second (Fig. 68a). More information could be expected if the search is extended to other specimens. Swamy and Bailey (1949) depicted a male inflorescence that is easier to interpret since groups of several stamens are situated in the axils of two successive pairs of bracts. Here all flowers seem to consist of eight to 13 stamens.

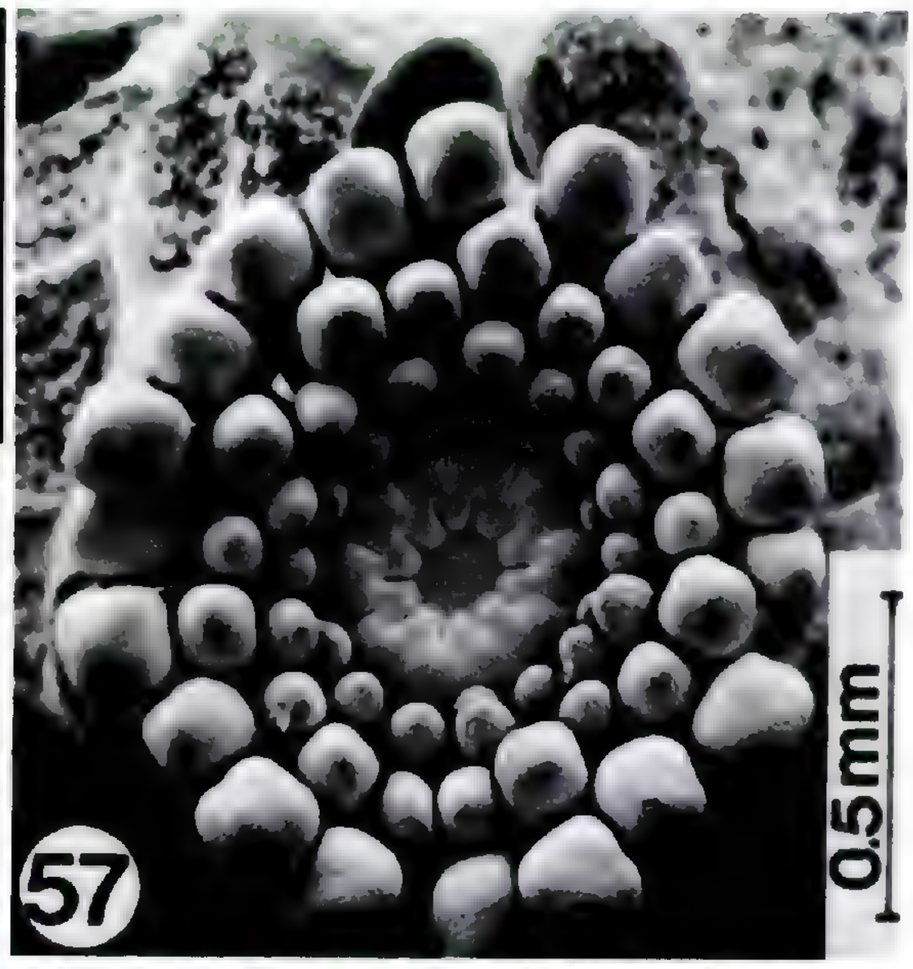
SOME HISTOLOGICAL FLORAL FEATURES OF SYSTEMATIC INTEREST

In *Tetracentron* all floral organs contain scattered enlarged cells with the contents dissolved in the fixed and sectioned material (Fig. 70). They much resemble the so-called "oil" cells that are generally present in many Magnoliidae, but absent in Hamamelidae. They are often more or less spherical as in Magnoliidae, apparently in contrast to the vegetative region where they have been described as elongate or branching by Bailey and Nast (1945), or termed "Sekretschläuche" by Harms (1897).

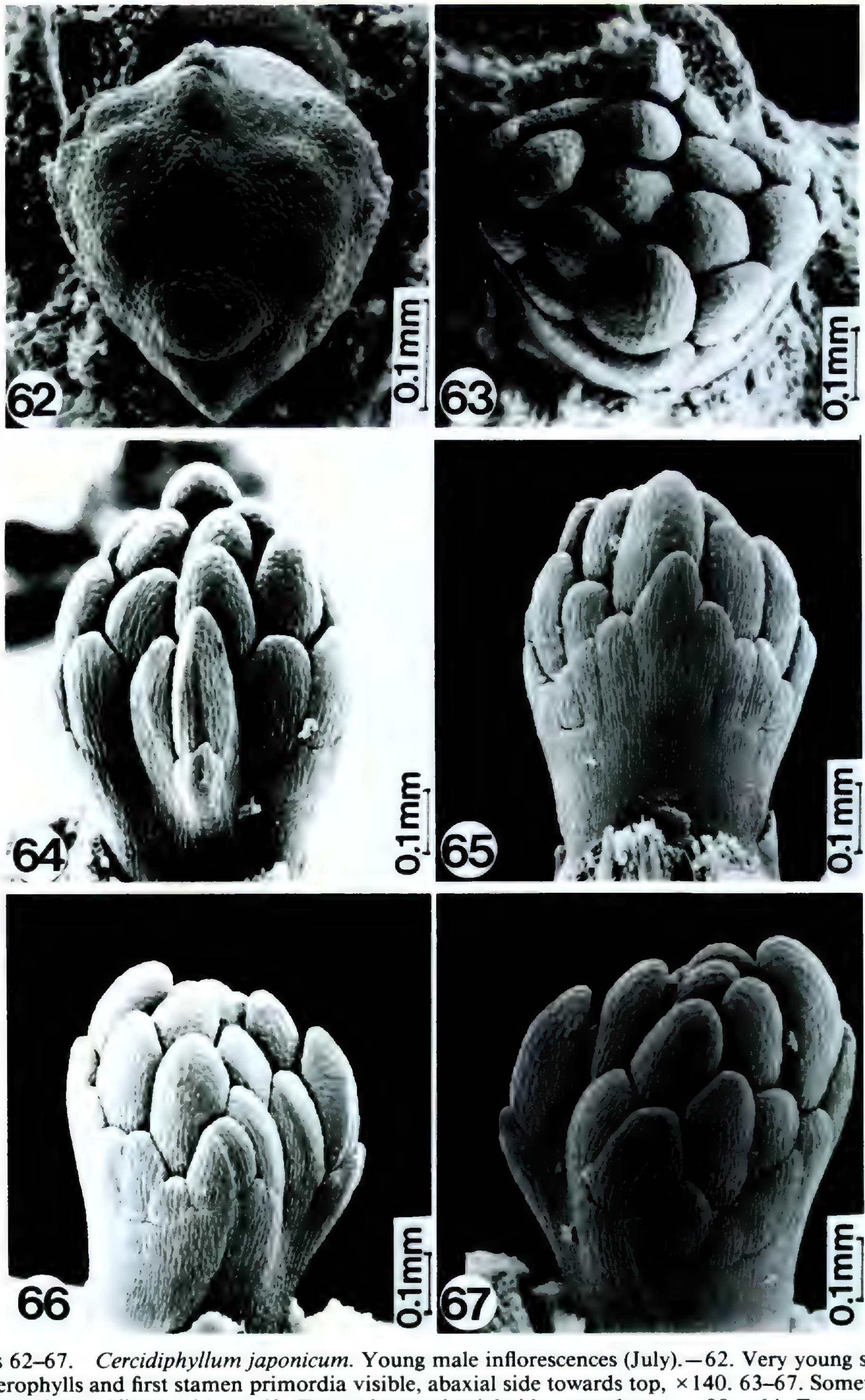
In *Trochodendron* similar cells differentiate into sclerified, branched idioblasts. However, in the gynoecium, at least at anthesis, many of these cells are not sclerified and presumably also correspond to "oil" cells (Fig. 71).

In addition, the tissues of the anthetic floral organs of both *Tetracentron* and *Trochodendron* are heavily tanniferous (Figs. 54, 55, 70, 71), but

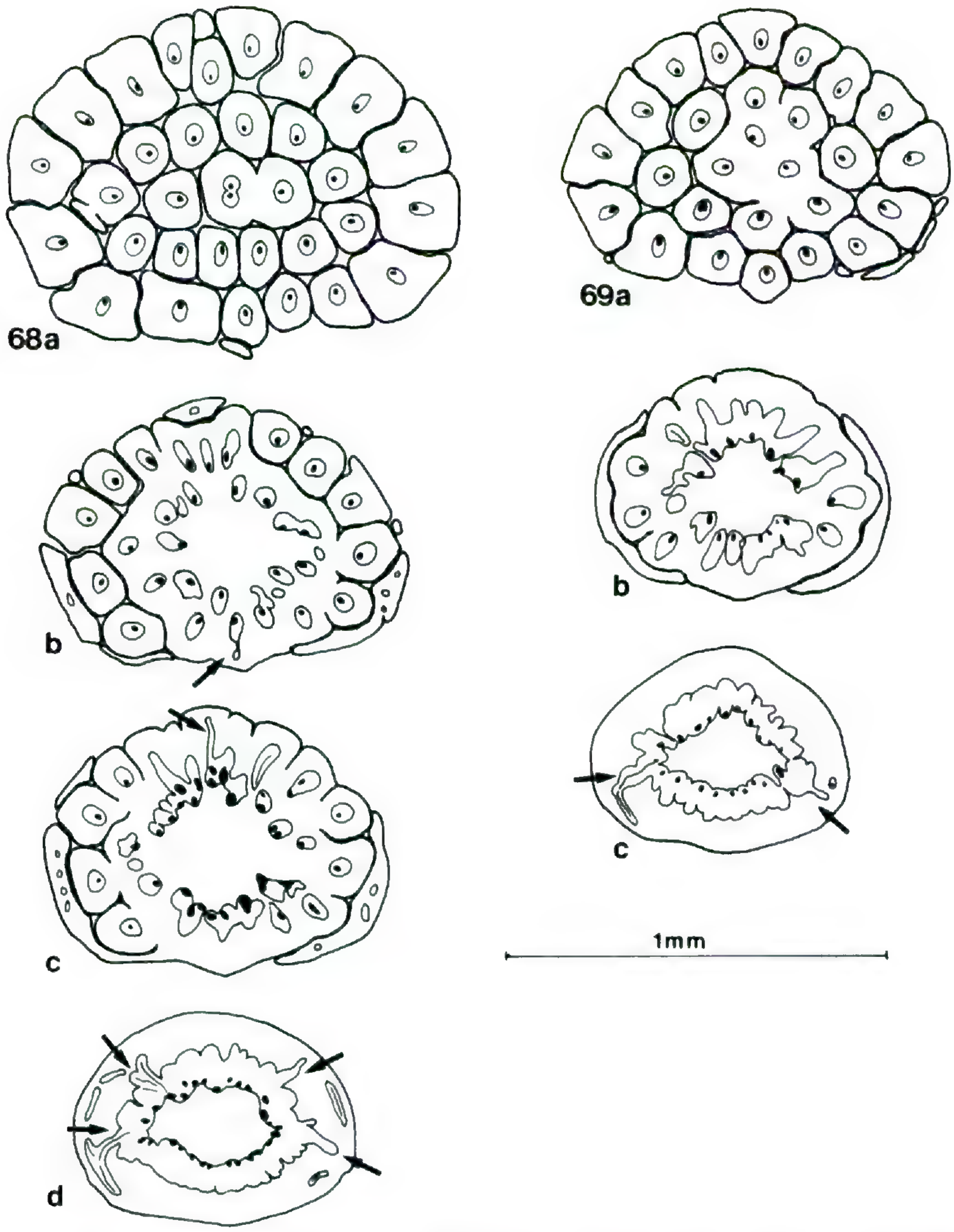




FIGURES 56–61. 56, 57. *Trochodendron aralioides*. Flowers of a young inflorescence (August) from above.—56. Lateral zygomorphic flower, ×55.—57. Terminal radially symmetric flower, ×40. 58, 59. *Euptelea polyandra* (July).—58. Young inflorescence from above, floral pherophylls removed to show floral primordia, ×30.—59. Same, enlarged; one zygomorphic flower with stamen primordia (larger on adaxial side), ×110. 60, 61. *Cercidiphyllum japonicum*. Young female inflorescence (July) with three unicarpellate flowers, the carpel clefts oriented towards their pherophylls.—60. From above, ×120.—61. From the abaxial side, median carpel (flower) without pherophyll, ×110.



FIGURES 62–67. *Cercidiphyllum japonicum*. Young male inflorescences (July).—62. Very young stage, from above, pherophylls and first stamen primordia visible, abaxial side towards top, ×140. 63–67. Somewhat older stage, viewed from different sides.—63. From above, abaxial side towards top, ×90.—64. From the abaxial side, ×85.—65. From the adaxial side, ×90.—66. From lateral (right side of Fig. 63), ×80.—67. From lateral (left side of Fig. 63), ×90.



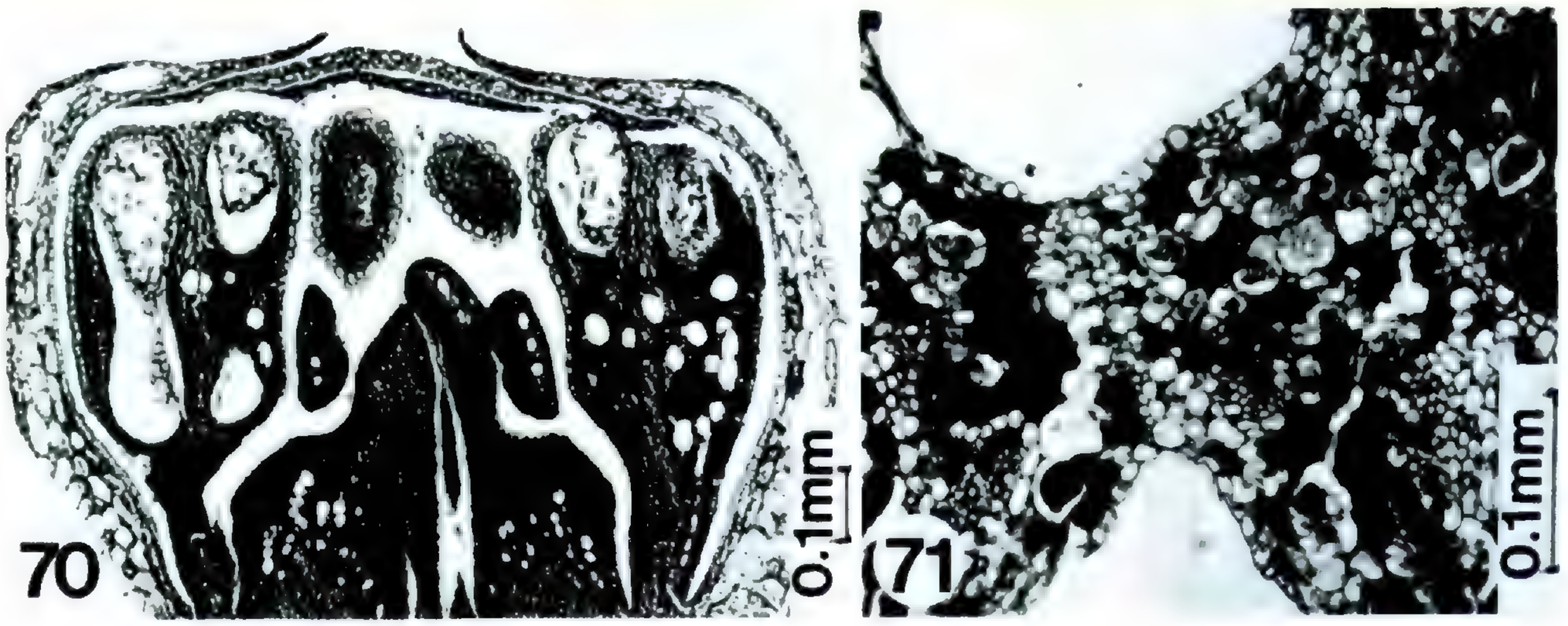
FIGURES 68, 69. *Cercidiphyllum japonicum.* Young male inflorescences, series of transverse sections.—68. Inflorescence with pherophylls on adaxial and abaxial sides: a, level with uppermost stamens becoming free from floral base; b, vascular trace of pherophyll of abaxial side joining a stamen bundle (arrow); c, vascular trace of pherophyll of adaxial side joining a stamen bundle (arrow); d, vascular traces of lateral pherophylls joining vascular stele of inflorescence (arrows).—69. Inflorescence without pherophylls on median side: a, level with uppermost stamens becoming free from floral base; b, level of free lateral pherophylls; c, vascular traces of lateral pherophylls joining vascular stele of inflorescence (arrows).

less so in *Euptelea* and *Cercidiphyllum.* A high tannin content is also typical for the flowers of Hamamelidales and many Magnoliales.

CONCLUSIONS

CIRCUMSCRIPTION OF TROCHODENDRALES

From our present knowledge it is evident that Trochodendrales sensu lato (including *Trochodendron, Tetracentron, Euptelea,* and *Cercidiphyllum*) are clearly related and form a coherent group because in none of the four genera can a relative be found in another order that would be more close than any of the three other genera. It is true that the extremes are relatively far apart. There is a relatively large step in floral structure between *Tetracentron* and *Cercidiphyllum.* However, in vegetative morphology the two genera resemble each other so much that the relationship is instantaneously evident. Furthermore, the meristic variation in floral organs *is* a typical constitutive feature of primitive angiosperms. The range in floral structure within the four genera is of about the same level as within the Hamamelidales sensu stricto (Hamamelidaceae, Platanaceae, possibly Myrothamnaceae). Therefore,



FIGURES 70, 71. "Oil" cells in floral tissue.—70. *Tetracentron sinense*; longitudinal section of old floral bud, "oil" cells present in all organs, ×55.—71. *Trochodendron aralioides*; transverse section of ovary at anthesis, ×140.

the four genera are formally best treated as an order Trochodendrales (like Dahlgren, 1980, but not 1983).

CLASSIFICATION OF THE TROCHODENDRALES

Of the four extant genera, *Trochodendron* and *Tetracentron* are the two most closely related. The present investigation shows that they are much more similar than has been pointed out earlier. This is reflected in Table 1. The most distinctive resemblances include: occurrence of a perianth (although rudimentary in *Trochodendron*), markedly valvate anther dehiscence, presence of a nectary on the carpellary dorsal bulges containing many sunken stomata surrounded by a ring of epidermal cells with heavily sculptured cuticle (all new characters); additionally, the very similar and distinctive pollen, ovaries and ovules, fruits and seeds, and also the similar vesselless wood and similar stomata in the vegetative body (Bondeson, 1952; Baranowa, 1983).

All this strongly points to the inclusion of both genera, *Trochodendron* and *Tetracentron*, in the same family Trochodendraceae (as suggested earlier by Gundersen, 1950, or—before the inflation of taxonomic group numbers on all hierarchic levels—by Hallier, 1903b: Trochodendreae of Hamamelidaceae). The remaining two genera of the order, *Euptelea* and *Cercidiphyllum*, may remain in separate families. Therefore, for the moment, a fairly balanced classification of the group would be as follows:

Trochodendrales	
Trochodendraceae	*Trochodendron*
	Tetracentron
Eupteleaceae	*Euptelea*
Cercidiphyllaceae	*Cercidiphyllum*

FOSSIL RECORD OF THE TROCHODENDRALES

Today, all four genera of the Trochodendrales are restricted to more or less small areas in temperate or subtropical Eastern Asia from Nepal (*Tetracentron*) to Taiwan (*Trochodendron*) and Japan (*Cercidiphyllum, Euptelea, Trochodendron*).

Cercidiphyllum was widely distributed in the Northern Hemisphere in the Tertiary (newer finds and reviews, e.g., Brown, 1962; Hummel, 1971; Becker, 1973; Chandrasekharan, 1974; Iljinskaja, 1974; Jähnichen et al., 1980; Scott & Wheeler, 1982; Basinger & Dilcher, 1983; Hickey et al., 1983; Stockey & Crane, 1983) and perhaps back to the Upper Cretaceous (Maestrichtian) (Hickey et al., 1983). In the Paleocene other genera were affiliated with *Cercidiphyllum*, such as *Joffrea* (Crane & Stockey, 1985) and with less certainty *Jenkinsella* (Chandler, 1964; Crane, 1978). Retallack and Dilcher (1981) even pointed to similarities between early *Cercidiphyllum* and the mid-Cretaceous genus *Prisca*.

Fossils of the three other genera can be identified with less certainty. Fossil leaves have been compared (with doubts) with *Trochodendron* and *Tetracentron* as far back as to the mid-Cretaceous (Iljinskaja, 1972, 1974). *Tetracentron*-like wood has been described from the Upper Cretaceous (Page, 1968). Wood ascribed to *Euptelea* was found in the early Tertiary of North America (survey in Wolfe, 1973).

The combined presence of leaves, fruits, and seeds of *Cercidiphyllum* in various fossil beds

TABLE 1. Character states occurring in more than one but not in all genera of the Trochodendrales to show their relationships.

Tetracentron	*Trochodendron*	*Euptelea*	*Cercidiphyllum*
entomophilous nectaries on carpel dorsal surface short anthers, short connective tips anther dehiscence markedly valvate pollen 10–15 μm diam. exine striate-rugulate apertures (colpi) long ovules mature at anthesis		anemophilous nectaries lacking long anthers, long connective tips anther dehiscence longitudinal or slightly valvate pollen 20–30 μm diam. exine finely reticulate and scabrate apertures short ovules immature at anthesis	
carpels sessile		carpels stipitate	
gynoecium syncarpous		gynoecium apocarpous or unicarpellate	
ovary semi-inferior		ovary superior	
seed coat 5-layered, middle layer sclerified		seed coat multilayered	
phyllomes between prophylls and stamens present (tepals)		phyllomes between prophylls and stamens lacking	
floral prophylls regularly present		floral prophylls lacking or present in basal flowers only	
"oil" cells present in floral organs		"oil" cells lacking	
wood without vessels		wood with vessels	
carpels weakly peltate	carpels strongly peltate	carpels epeltate	
pollen triaperturate fruits dehiscent seeds with appendages	pollen pluriaperturate fruits indehiscent seeds without appendages	pollen triaperturate fruits dehiscent seeds with appendages	
flowers bisexual leaves alternate		flowers unisexual leaves opposite	
stamens 4 flowers enclosed by perianth in bud carpels 4	stamens numerous flowers enclosed by cataphylls in bud		
flowers sessile stipules present 1-leaved short shoots present	carpels numerous flowers pedicelled stipules absent 1-leaved short shoots lacking	carpel 1 flowers sessile stipules present 1-leaved short shoots present	
leaves deciduous	leaves evergreen	leaves deciduous	

TABLE 2. Character states of the Trochodendrales shared with certain Magnoliidae or Hamamelidae to show their relationships. Some of the character states occur in both subclasses but are more important on the side where they are mentioned. The initials of the genera of Trochodendrales are mentioned in brackets if a feature does not occur in the other ones (C, *Cercidiphyllum*; E, *Euptelea*; Te, *Tetracentron*; Tr, *Trochodendron*).

Magnoliidae	Trochodendrales	Hamamelidae
carpel number with wide range		
carpel stipitate, style lacking (E)		
nectary on carpel dorsal surface (Te, Tr)		
stigma with unicellular papillae		
wood vesselless (Te, Tr)		
"oil" cells present (Te, Tr)		
single adaxial prophyll (C)		
chloranthoid leaf teeth (Te, Tr, C)[1]		
plants more or less glabrous		
lack of myricetin[2]		
	anther dehiscence valvate (Te, Tr, E)	
	filaments long	
	pollen tri- or pluriaperturate with marked apertural exine structure	
	ovary semi-inferior (Te, Tr)	
	ovules immature at anthesis (E, C)	
	fruits dehiscing, seeds edged and winged (Te, Tr, C)	
	presence of an unelaborated compitum in syncarpous taxa (Te, Tr)	
	stipules present (Te, C)	

[1] Hickey and Wolfe (1975).
[2] Kubitzki and Reznik (1966).

facilitates the identification of the material. That the fruits and seeds of *Cercidiphyllum* are better suited to fossil preservation than those of the other three genera is probably due to their more robust texture and flat shape limiting deformation.

All these many finds, especially those of *Cercidiphyllum* and extinct genera related to it with an obviously much wider distribution and greater diversification in the early Tertiary corroborate the impression that the Trochodendrales are a relic group with a long history, and are now in the state approaching extinction. Present modest diversity on the generic level (*Euptelea* and *Cercidiphyllum* with two species each) points to relatively recent differentiations.

POSITION OF THE TROCHODENDRALES BETWEEN THE MAGNOLIIDAE AND HAMAMELIDAE

The Trochodendrales are closely related to Magnoliales and at the same time to Hamamelidales. The Trochodendrales are intermediate between the core Magnoliidae and Rosidae/Hamamelidae (Table 2): Some have retained vesselless wood and "oil" cells, but they have already acquired tricolpate pollen and valvate anthers of a hamamelidalian type. The odd female flowers of *Cercidiphyllum* consisting of a single carpel fall rather in the range of Magnoliidae than Hamamelidae. The distance to the core Magnoliales and Hamamelidales is about the same for all four genera, but for each from different angles. Additional embryological features not mentioned in the text, sieve tube plastid differentiation or chromosome numbers do not contribute much to this special question because they are too uniform in the critical groups under consideration here (Yakovlev, 1981; Ly-thi-Ba, 1981; Behnke, 1981) or too diverse (Ratter & Milne, 1973, 1976).

The perianth may be seen as a marker trait. In the Magnoliales the perianth is not yet differentiated into typical sepals and petals (cf. Hiepko, 1965). In the Trochodendrales the perianth is reduced, whereas in the Rosales/Hamamelidales it is often differentiated into sepals and petals, sometimes also reduced (at least partly

from a double perianth, cf. Endress, 1977; see also Ehrendorfer, 1977).

It seems reasonable that the Trochodendrales evolved from an ancestral group which had a perianth, but not yet differentiated into sepals and petals, as in Magnoliales. The Hamamelidales, in contrast, originated from a group where a well-differentiated perianth with sepals and petals already occurred, but petals *and* sepals were secondarily lost in many taxa.

On the whole, the Trochodendrales are not ancestral to the Hamamelidales. They are a conservative, isolated group. However, they have common roots with Hamamelidales and have retained more magnolialian traits than have the Hamamelidales.

Therefore, the formal inclusion of Trochodendrales in either Magnoliidae or Hamamelidae can be justified. An inclusion in the Hamamelidae seems reasonable (if this subclass is retained as such at all) because it is a smaller subclass than Magnoliidae.

The urgent need now is a detailed comparative study of all families of Magnoliidae and Hamamelidae, and not a premature phenetic or cladistic classification solely from the available information in the literature. Our ultimate goal is better knowledge of the living plants and better understanding of their phylogeny.

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THE FLORAL MORPHOLOGY AND VASCULAR ANATOMY OF THE HAMAMELIDACEAE: SUBFAMILY LIQUIDAMBAROIDEAE[1]

A. LINN BOGLE[2]

ABSTRACT

Inflorescence and floral morphology and floral vascular anatomy of the subfamily Liquidambaroideae (*Liquidambar* L., *Altingia* Nor.) are described. The inflorescence appears to be a greatly condensed compound raceme with proximal pistillate heads and distal staminate heads. Functionally pistillate flowers contain sterile or even fertile stamens. Functionally staminate flowers may show evidence of partially developed gynoecia. There is no morphological or anatomical evidence of sepals or petals. In functionally pistillate flowers a cycle of sterile phyllomes of uncertain nature (staminodia?, disc lobes?) is inserted on the hypanthium between the stamens and carpels of the partly inferior ovary. In pistillate flowers the stamens derive a single trace and the phyllomes a ramifying system of bundles from hypanthial trunk bundles. Each carpel contains a dorsal and two ventral bundles. Numerous ovules on each carpel margin receive traces from the ventral bundles. The gynoecium is interpreted as the most primitive within the Hamamelidaceae, and subfamilial status of Liquidambaroideae, rather than segregation as the family Altingiaceae, is supported.

There has been an increase in interest and discussion in recent years concerning the nature and origins of the "Amentiferae"—a group now accepted by a majority of modern systematists as being made up of highly advanced and specialized taxa—and how they relate to more primitive groups of angiosperms. Central to this problem are the nature and position of the family Hamamelidaceae, which occupies an intermediate position in the various theories and phylogenetic schemes that have been put forth. However, any considerations of the phylogenetic position of the Hamamelidaceae, and of the trends of specialization both within and without the family, must begin with a reasonably clear understanding of which members of the family are primitive, or most nearly so, and which are advanced. At present, opinion is divided on this point and on circumscription of the family. This is due to the remarkable morphological diversity evident among the 28–30 genera that are now known to comprise the five distinct subfamilies traditionally included in the family. Such diversity is particularly evident among the seven genera that make up the four small subfamilies Liquidambaroideae (Altingioideae of Cronquist, 1981), Rhodoleioideae, Exbucklandioideae (formerly Bucklandioideae or Symingtonioideae of some authors, including Chunioideae of Takhtajan, 1980, and Mytilarioideae of H. T. Chang, 1973), and Disanthoideae.

Each of these subfamilies, and the Liquidambaroideae in particular, is characterized by interesting combinations of primitive and advanced morphological and anatomical features that have led to varying interpretations of their relationships and relative phylogenetic positions. Thus, *Altingia* and *Liquidambar*, comprising the subfamily Liquidambaroideae, have been removed by some workers (e.g., Blume, 1828;

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Hayne, 1830; Lindley, 1836; Wilson, 1905; C. T. Chang, 1959, 1964; Melikian, 1971, 1973a, 1973b; P. R. M. Rao, 1974; T. A. Rao & Bhupal, 1974; Skvortsova, 1960) from the Hamamelidaceae as a segregate family Altingiaceae. Others have considered *Liquidambar* and *Altingia* to be relatively primitive taxa within the Hamamelidaceae (e.g., Makarova, 1957; Schmitt, 1965; Meeuse, 1975), whereas such recent authors as Schulze-Menz (1964), Cronquist (1968), and Takhtajan (1969) considered these genera as relatively advanced members of the Hamamelidaceae. Similarly, Willis (1966) and Wolfe (1973) segregated *Rhodoleia* as a family Rhodoleiaceae, principally on the basis of leaf architecture. Cronquist (1968), while maintaining the Hamamelidaceae in the broad sense, stated that "the monotypic genus *Disanthus* has at least as much claim to family status as the Altingiaceae." The most extreme position is that of Nakai (1943), who went so far as to elevate all four subfamilies to family status, thus restricting the Hamamelidaceae to the genera of subfamily Hamamelidoideae.

With regard to what constitutes the most primitive floral type within the family, Takhtajan (1969) stated that *Disanthus cercidifolius* Maxim., the sole member of the subfamily Disanthoideae, "is the most primitive in floral structure." Cronquist (1968) considered *Disanthus* as "clearly the most primitive" genus in the family, or (Cronquist, 1981) that it "may be the most archaic surviving genus." This view of the primitive nature of *Disanthus* is concurred in by Wolfe (1973) on the basis of leaf architecture (apparently assuming the exclusion of *Rhodoleia* from the Hamamelidaceae), and by Goldblatt and Endress (1977) on evidence from chromosome counts.

Unfortunately, there is still relatively little basic information available in the literature from comparative morphological and anatomical studies of a comprehensive nature on these relatively primitive members of the family. More data are needed before suppositions concerning primitive or advanced conditions, and the morphological limits of the Hamamelidaceae, can be made with any assurance and employed in considerations of extrafamilial relationships.

This paper is intended to present an account of the floral morphology and vascular anatomy of the two genera comprising the subfamily Liquidambaroideae (*Liquidambar, Altingia*) based on original anatomical work and morphological observations, as part of an effort to provide comparable data for all genera of the family. Some observations concerning the little known segregate genus *Semiliquidambar* are also presented.

MATERIALS AND METHODS

Inflorescences of *Liquidambar* and *Altingia* in various stages of development have been collected from both wild and cultivated trees in southeast Asia, and North America either by me, or for me by others. In addition, inflorescences from herbarium specimens in the Arnold Arboretum (A) have also been examined, including those attributable to *Semiliquidambar*. The specimens examined, collection data, and location of voucher specimens are listed in Table 1.

The methods of preservation, preparation and staining of sections, and clearing of floral parts are standard and have been described previously (Bogle, 1970).

I have examined both sectioned and cleared specimens of staminate and pistillate flowers and inflorescences of *Liquidambar* and *Altingia* in anthesis and post anthesis stages.

Drawings were made with the aid of the drawing attachments designed for the Wild M-20 and M-5 microscopes.

I am grateful to the directors and curators of the following aboreta and herbaria for permitting me to use their living and herbarium collections, and for supplying material for the study: Arnold Arboretum of Harvard University; Gray Herbarium of Harvard University; Morris Arboretum of the University of Pennsylvania; Scott Foundation of Swarthmore College; University of Washington Arboretum, Seattle; and the Royal Botanic Gardens, Kew, Great Britain.

RESULTS

In the following paragraphs, the descriptions of the vasculature of the functionally pistillate flowers (hereafter referred to simply as pistillate flowers) are based primarily on serial sections, whereas those of the functionally staminate flowers (hereafter referred to simply as staminate flowers) are based primarily on cleared material. Emphasis is given here to the functionally pistillate flowers because these are, in fact, morphologically and sometimes functionally perfect and more useful for comparison with flowers of the other subfamilies. The staminate flowers, in contrast, appear to represent the culmination of a line of reduction from the perfect condition within the subfamily.

TABLE 1. Collections on which anatomical and morphological observations presented here are directly based (A = Arnold Arboretum, ALB = author's collection).

Taxon	Collector	Locality	Deposited
Altingia chinensis (Champ.) Oliver	*Bogle 583*	Hong Kong Botanical Garden	ALB
	Bogle 588	Hong Kong, forest above Peel Rise, off Aberdeen Road	ALB
	Bogle 591	Hong Kong, forest above Peel Rise, off Aberdeen Road	ALB
	Hu 6700	Hong Kong	ALB
	Pételot 5944	Tonkin, Chapa, 1,500 m	A
Altingia chingii Metc.	*Lau 4356* (paratype)	China, Kiangsi	A
	Tso 20760	China, N. Kwangtung, Lok Chong, Yao Shan	A
Altingia excelsa Nor.	*Bogle 313*	Malaya, Pahang, Cameron Highlands, Mentigi Forest Reserve	ALB
	Abbe 10298	Malaya, Pahang, Cameron Highlands, Mentigi Forest Reserve	ALB
Liquidambar formosana Hance	*Bogle 610*	Taiwan, Yin-Ping, between Chitow and Chushan	ALB
Liquidambar orientalis Mill.	*Bogle 973*	USA, Minnesota, Minneapolis, cultivated specimen in Univ. of Minnesota greenhouse	ALB
Liquidambar styraciflua L.	*Bogle 790*	USA, Pennsylvania, Montgomery Co., Willow Grove, Red Barn Road	ALB
	Bogle 823	Mexico, Hidalgo, vic. El Barrio Road, km 322, S of Tamazunchale	ALB

SUBFAMILY LIQUIDAMBAROIDEAE

Two (or three) genera of large trees make up this distinctive subfamily. The most well known of these, and the most widespread in both living and fossil form, is *Liquidambar* L., which is characterized by its palmately-lobed and -veined, deciduous leaves. *Liquidambar* is disjunctly distributed in eastern Asia, Asia Minor, and in North and Central America.

Less well known is *Altingia* Nor., which differs from *Liquidambar* in its simple, elliptic to oblong, pinnately-veined, evergreen leaves. *Altingia* is widely distributed in southeast Asia.

The segregate genus *Semiliquidambar* H. T. Chang (including *Altingia chingii* Metc.) was established (H. T. Chang, 1962, 1973) to include specimens whose leaf morphology is intermediate between that of *Altingia* and *Liquidambar*. These species are described as having leaf blades that vary from undivided to 2- or 3-lobed, triplinervous venation, and with pistillate flowers lacking staminodia, among other morphological features. I have seen specimens of *Altingia chingii* in which the leaves appear to bridge the gap in leaf shape between *Altingia* and *Liquidambar* (*Tso 20760*, paratype, A; *Lau 4356*, A; see also Metcalf, 1931, pl. 58; and description of *A. chingii* var. *parvifolia* in Chun, 1934). These genera are in need of monographic revision to better define the number of species and clarify the validity of *Semiliquidambar*. I have not had access to floral material of *Semiliquidambar* suitable for detailed morphological and anatomical work.

Liquidambar and *Altingia* share several morphological and anatomical characteristics, including: gum ducts associated with the vascular bundles of the stems, leaves, and floral organs; formation of terminal buds enclosed within numerous bud scales; spirally arranged stipulate leaves; stipules mounted on the petiole rather than on the stem; extremely condensed, complex, bisexual inflorescences containing numerous many-flowered heads; flowers naked, perfect, or imperfect, and functionally pistillate or staminate; a cycle of sterile organs surrounding the ovary in pistillate flowers; pollen grains polyporate (forate); ovules numerous, inserted on both carpel margins, but only the lowermost one or two on each margin fertile; and seeds winged. This *combination* of characteristics sets the

subfamily quite apart from the rest of the family, but specific characteristics (e.g., gum ducts, complex inflorescences, sterile floral organs, polyporate pollen grains) do occur in certain genera of the other subfamilies, so are not unique to the *Liquidambaroideae*. For descriptive purposes I shall use the generalized term *phyllome* (cf. Esau, 1965: 424) in reference to the cycle of sterile organs as they appear in *Liquidambar* and *Altingia*, because they are not clearly either staminodial or carpellary in nature.

1. Liquidambar L., Sp. Pl. 2: 999. 1753. Figures 1A, 2, 3, 4A–F, 6A–D, I, J.

The genus *Liquidambar* consists of two to five species of large deciduous trees distributed in the Northern Hemisphere. *Liquidambar formosana* Hance is widespread in eastern Asia (Tardieu-Blot, 1965; Li, 1977; H. T. Chang, 1962, 1973). *Liquidambar acalycina* occurs in at least nine provinces of China (H. T. Chang, 1973, 1979). *Liquidambar orientalis* Mill. is known from Turkey and some islands of the Aegean Sea such as Rhodes (Rechinger, 1943) and Cyprus (Holmboe, 1914; Meikle, 1977, as *L. styraciflua*). *Liquidambar styraciflua* L. is widely distributed in eastern and southeastern North America and southward at high elevations on the mountains of Mexico and Central America to Honduras (Little, 1971, map 135-E, 135-N). The Mexican and Central American plants are recognized by some authors as a distinct species, *L. macrophyllum* Oerst. (Sosa, 1978). The three principal species (*L. formosana, L. orientalis, L. styraciflua*) are also widely cultivated as ornamental trees and form the basis for my observations.

The stipulate leaves of all three species are palmately-lobed and -veined, but differ in the degree of lobation and pubescence. The leaves of *Liquidambar formosana* are usually 3-lobed, those of *L. styraciflua* are usually 5(–7)-lobed (see Duncan, 1959, for a detailed analysis of leaf form in *L. styraciflua*), whereas those of *L. orientalis* are also 5(–7)-lobed, but with the lobes further subdivided. Leaf form in the last two species is intergrading, however, and some authors consider them conspecific (Rechinger, 1943; Meikle, 1977).

Harms (1930, see also H. T. Chang, 1979) recognized two sections within the genus. Section *Cathayambar* Harms, containing only *Liquidambar formosana* (Fig. 2A), is distinguished primarily by the presence in the pistillate inflorescences of elongate, fleshy, subulate, pubescent setae ("borsten") of varying length, which he interpreted as being "between the female flowers," whereas in section *Euliquidambar* Harms, containing *L. orientalis* and *L. styraciflua* (Fig. 3A), such setae are said to be lacking (H. T. Chang, 1979, also placed *L. acalycina* in this section).

Morphology. The flowers of *Liquidambar* are naked and usually functionally unisexual. They are fused in small, spherical to elongate heads that are spirally arranged in a narrowly conical, complex inflorescence. One to three long-pedunculate, pistillate heads occupy the basal nodes of the inflorescence (Fig. 1A), followed distally by numerous (ca. 15–20) short-pedunculate to sessile staminate heads (Figs. 1A, 4A, staminate portion of the inflorescence, bracts, and stamens removed to show axes). In some inflorescences a pistillate head may be lacking. The staminate and pistillate flowers and heads are usually distinct in form and function, but exceptional and intergrading forms are common. Some examples of such forms are discussed below in a brief consideration of the inflorescence following the morphological descriptions of typical pistillate and staminate flowers.

Pistillate flower. The functionally pistillate flowers are naked but perfect. Six to eight basal or sub-basal, elongate, hyaline bracts subtend the head and initially enclose it but quickly drop off after anthesis. I could find no morphological or anatomical evidence of either a calyx or corolla in any of the primordial or mature flowers examined.

The androecium of the pistillate flower consists of a cycle of five to eight (four to ten in Harms, 1930) stamens inserted at the angles of the floral periphery. The stamens vary in their degree of development from head to head. The anthers may be sessile or borne on short filaments and may range in form from strongly reduced and sterile (Figs. 2A, 3A) to fully developed anthers containing abundant sterile or even fertile pollen. When fertile, however, the anthers apparently do not dehisce until the stigmas of the same flower are well past their receptive period, thus preventing self-fertilization in these proterogynous female inflorescences (Schmitt, 1965).

The gynoecium consists of two (one to six) involute carpels that are fused below but apocarpous above, forming a syncarpous, half-inferior ovary. In the base of the ovary the fused

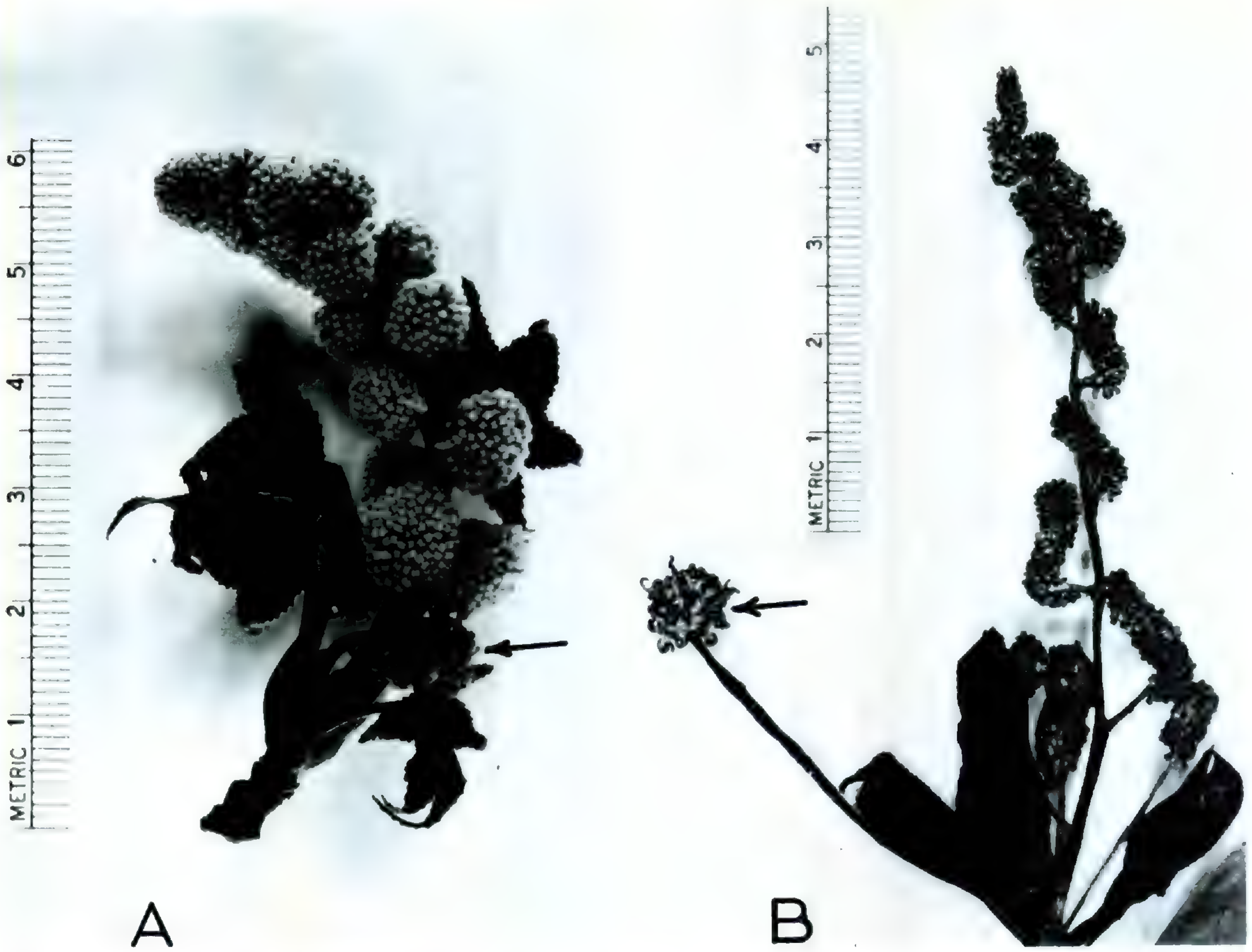
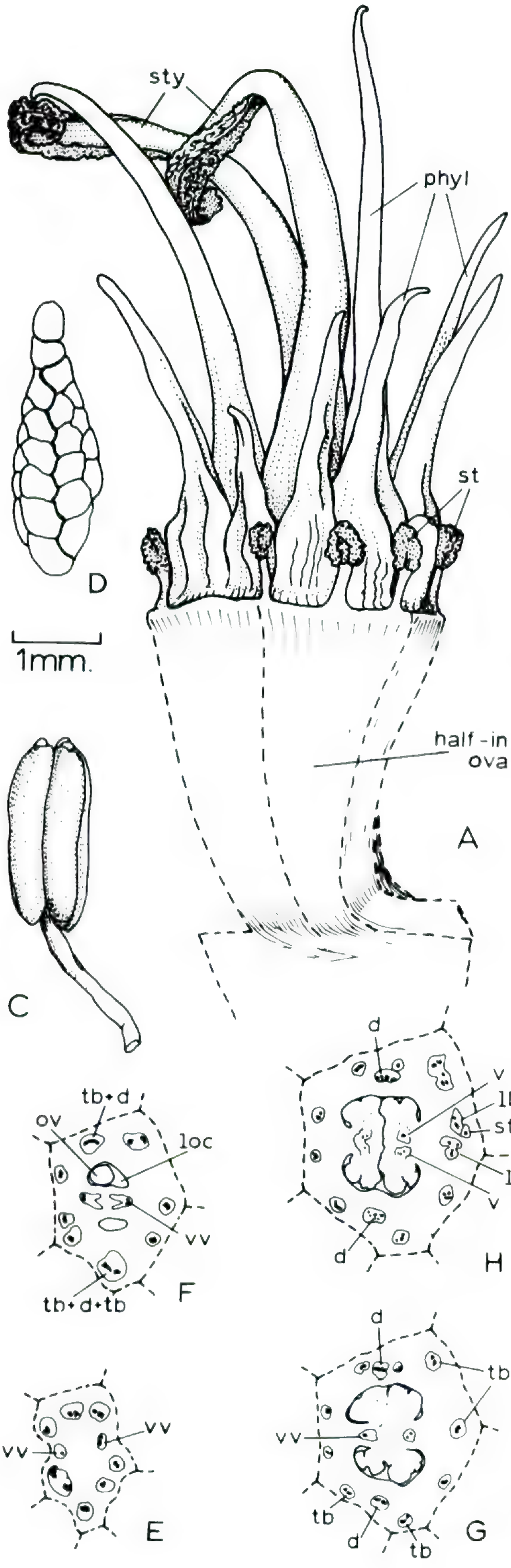


FIGURE 1.—A, B. Total inflorescences of *Liquidambar styraciflua* L. and *altingia chinensis* (Champ.) Oliv. The single, basal, pistillate head in each inflorescence is indicated by an arrow. All other heads are staminate.

carpel margins form a thick but shallow septum (Figs. 2F, G, 3E) that divides a short distance above the base of the locule to form two appressed, compound, parietal placentae (Figs. 2H, 3F, G).

Each carpel margin bears two rows of pendent, anatropous ovules. The number of ovules on each margin in my material ranges from ten to 15 in *Liquidambar formosana* (*Bogle 610,* Fig. 2D), and ten to 13 in *L. styraciflua* (*Bogle 790, 823,* "*L. macrophylla*") and *L. orientalis* (*Bogle 973*). The ovules are arranged in a double row on the central part of each carpel margin, giving way to single ovules above and below (Fig. 2D, see also Griffith, 1836, pl. XVI, as *Sedgewickia*). The ovules of *Liquidambar styraciflua* lack an egg apparatus at the time of pollen release (Schmitt & Perry, 1964). In transverse sections the ovary appears bilocular below but is essentially unilocular above the top of the septum, even though the tightly appressed placentae give the appearance of two locules. Above the septum the tightly appressed carpel margins are not sealed, and the carpels are thus "open" at pollination. Externally, the dorsal surfaces of the carpels become free from the hypanthium, and adaxially from each other, at a level slightly above the top of the septum (Figs. 2J, K, 3G–I). In the material I studied, the styles of *L. orientalis* and *L. styraciflua* (Fig. 3A) were notably shorter and stouter, and their stigmatic surfaces broader, than those of *L. formosana,* but the possibility of regional variation in style-stigma morphology in these species has not been ruled out.

Surrounding the base of the apocarpous portions of the carpels is a cycle of fleshy, sterile phyllomes (Fig. 2A) that are of particular interest because of the variety of interpretations that have been placed on them by various workers. In *Liquidambar formosana* these take the form of the long setae ("borsten" of Harms, 1930) that characterize section *Cathayambar.* Oliver (1867) described these structures as "long spines, produced from the calyx-limb . . . not at first sight readily distinguishable from the persistent indurated styles." Ek (1902) considered them to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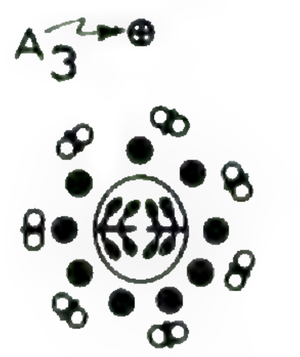
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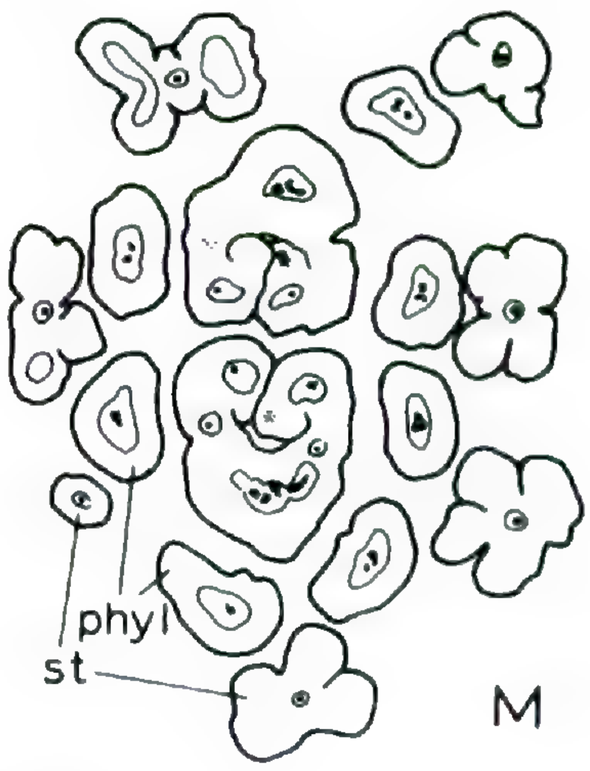
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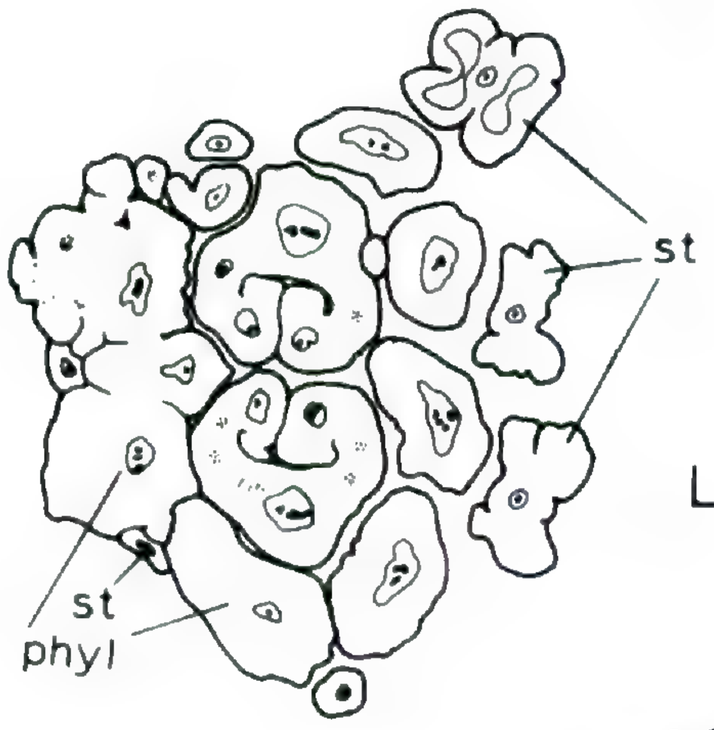
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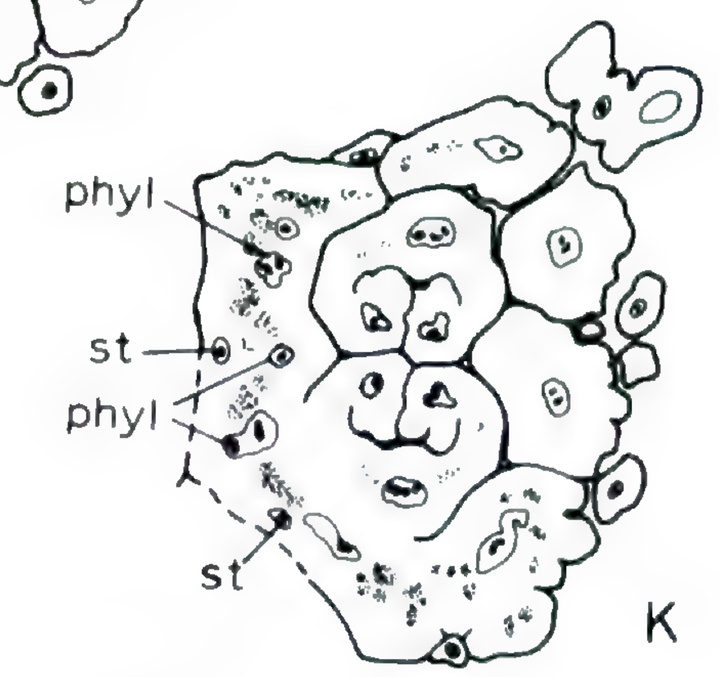
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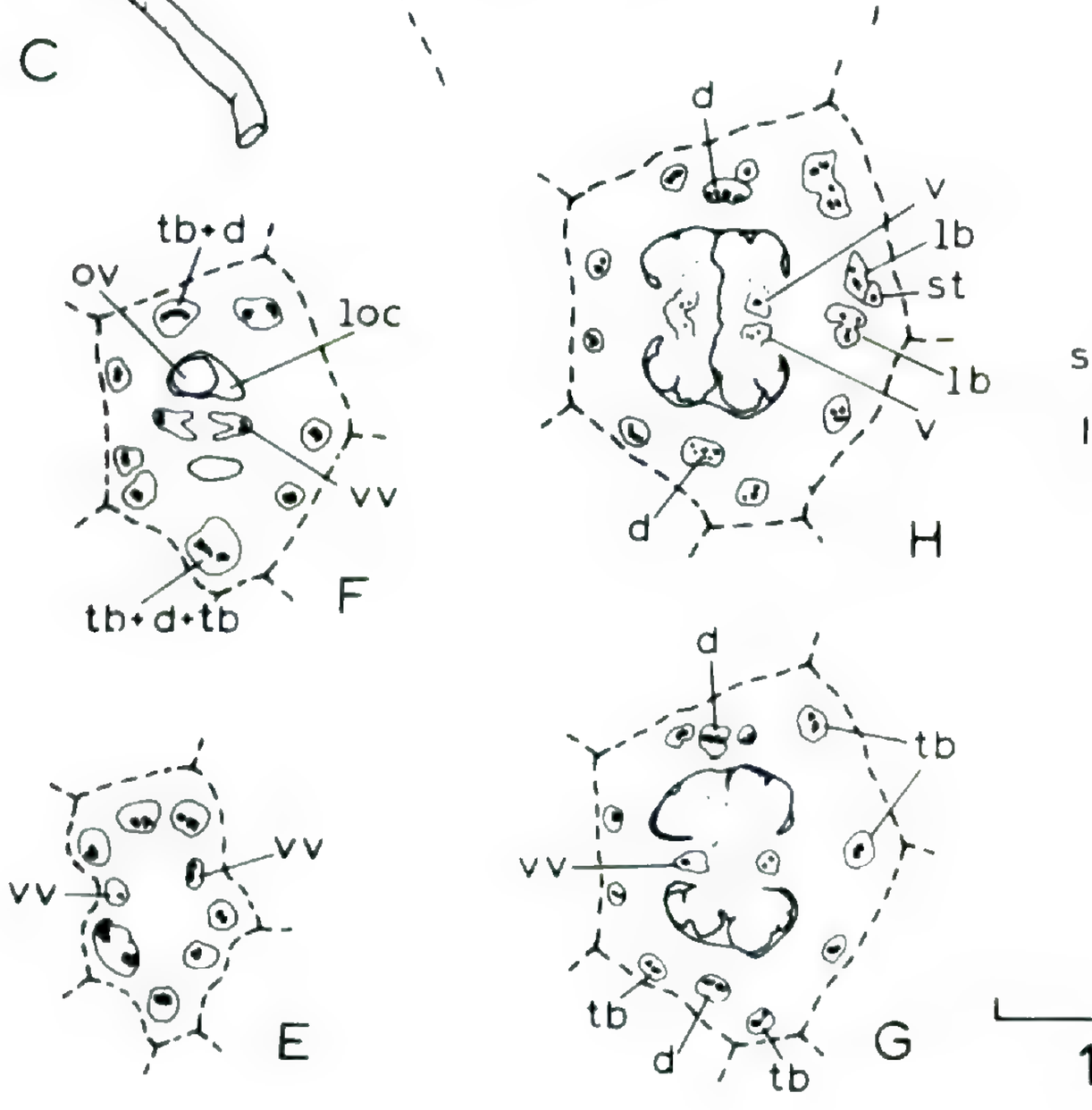
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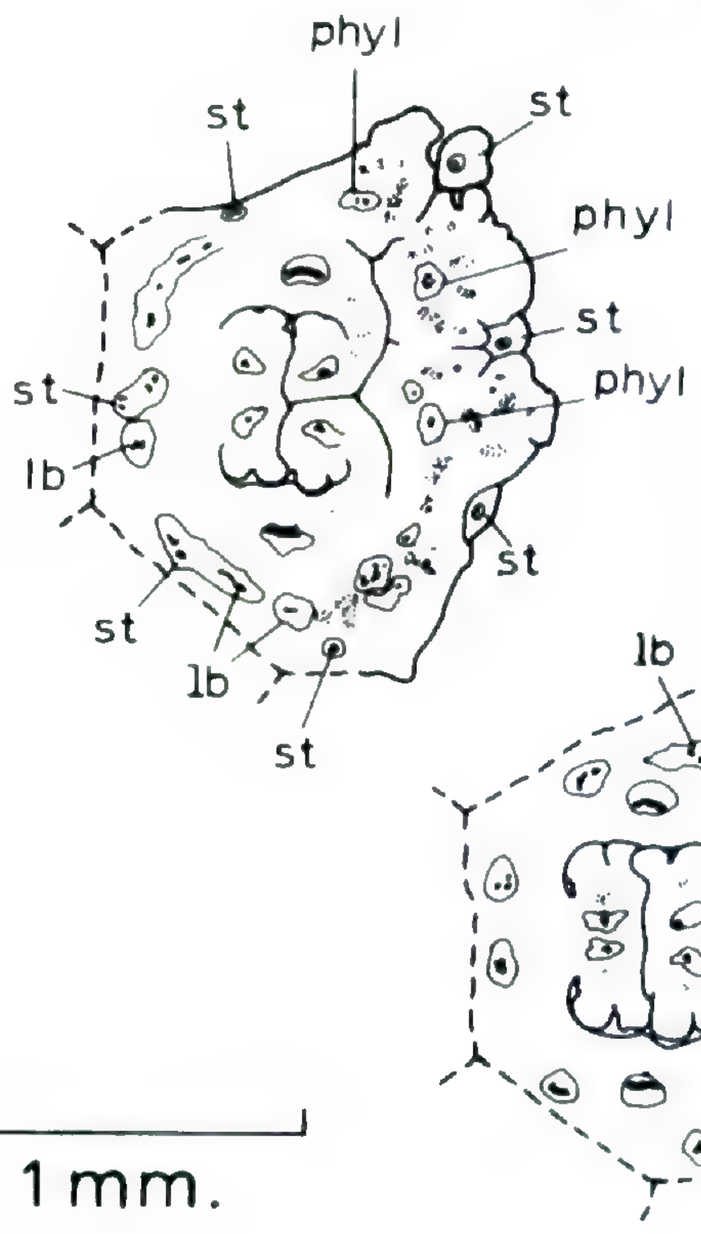
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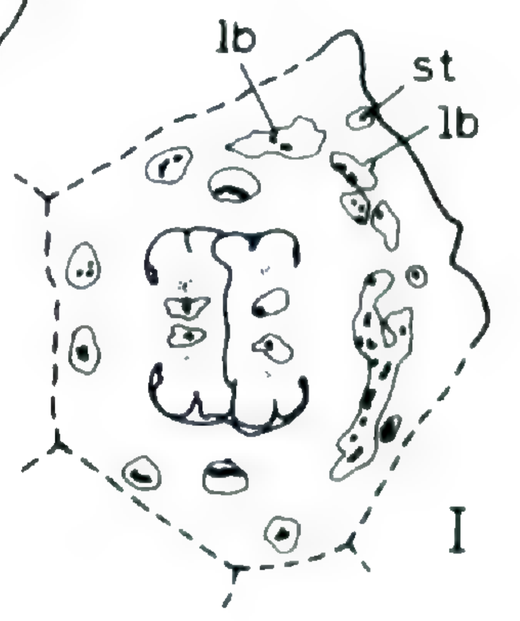
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be "isolated perianth parts." Guillaumin (1920) called them "bracteoles" surrounding the female flower, and Harms (1930) suggested that they are vestigial styles of sterile flowers inserted between the fertile flowers. These styliform bodies appear outwardly very much like the functional styles except for their variable size and the absence of stigmatic surfaces (cf. Fig. 2A). The two setae inserted on either side of the ovary in the median plane are usually the largest, perhaps reflecting a slightly greater amount of space for growth and enlargement in the angles between the two carpels. One of these setae is usually larger than its opposite number, often approaching the styles in length. In flowers of *L. orientalis* and *L. styraciflua* these sterile structures are reduced to a cycle of short, blunt, glabrous, fleshy lobes surrounding the carpels ("phyl" in Fig. 3A) and forming the "indistinct–broadly crenate, minutely warty, lobed, protrusive receptacle" described by Harms (1930). Schmitt (1965) described these organs in *L. styraciflua* as "papillae" that "form on the surface of the capsules."

Staminate flower. The naked staminate flowers (Fig. 4) are highly reduced and fused in spirally arranged, congested, bracteate (B_1) spikes, heads, or clusters along the primary inflorescence axis. Each head represents a secondary inflorescence axis (A_2), the larger of which axes, in turn, bear secondary bracts (B_2) with axillary flower clusters (Fig. 4, anthers removed from heads; A, *Liquidambar styraciflua*; B–F, *L. orientalis*). The staminate flowers may be strictly staminate or contain the merest vestiges of rudimentary carpels [Fig. 4B(5), note the partially developed styles and stigmas of several ovaries; 4C(3) and 4F, note tips of rudimentary carpels visible within cycle of stamens]. Each flower contains four to eight (to ten) stamens arranged in a single cycle, although the flowers and stamens are often so densely crowded that it is sometimes difficult to determine this detail of floral structure. I found no evidence in *L. orientalis* to support Ek's (1902) statement that each staminate flower consists of one stamen. There is no evidence in the typical staminate flower of the cycle of sterile phyllomes that is so prominent in the pistillate flower.

Near the base of each staminate head distortion of the flowers, due to such factors as reduction of the peduncle, fusion of the peduncle to the primary inflorescence axis, and differential growth, make it difficult, if not impossible, to delimit individual flowers. In the middle and distal portions of the head, however, it is often apparent that the stamens are arranged around shallow, pubescent, elongate pits or depressions in the surface of the axis [Fig. 4C(3)]. The pubescent tips of two abortive carpel primordia are frequently visible within the ring of stamens at either end of the pit. Tong (1930, fig. 10) noted such vestigial gynoecia in male flowers of *Liquidambar formosana.*

The mature fertile stamens (Figs. 2C, 3C) contain four sporangia and dehisce by means of two simple, lateral, longitudinal slits. At anthesis the pistillate heads are pendent on long peduncles, whereas the main axis of the total inflorescence, bearing the staminate heads, is more or less erect. After pollination the entire distal staminate portion of the inflorescence (Fig. 4A) quickly withers and drops away. The peduncles of the pistillate heads remain attached and the heads ripen and enlarge several-fold. Most of this enlargement is due to the growth of the numerous ovaries within the head, but part of it is apparently attributable to the activity of a vascular cambium in the axis of the head (Schmitt, 1965). The seeds are shed in the fall.

Inflorescence variation. Although staminate and pistillate heads are usually strongly differ-

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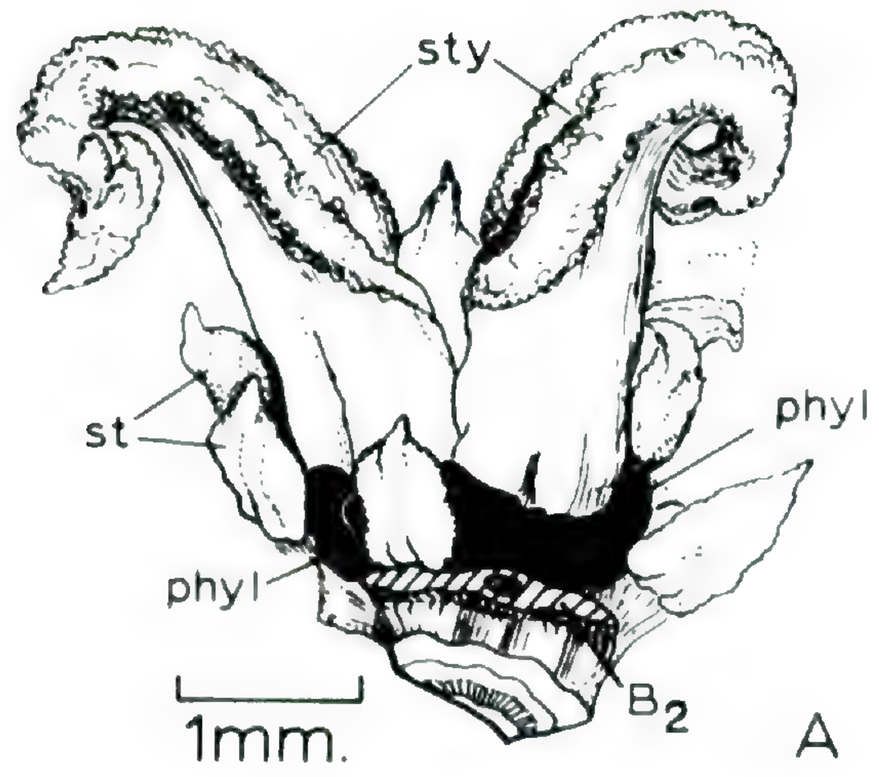
FIGURE 2. *Liquidambar formosana* Hance.—A. Pistillate flower at anthesis, excised from a head.—B. Floral diagram.—C. Stamen from a staminate flower.—D. Arrangement of ovules on margins of one carpel. E–M. Serial sections of a pistillate flower at anthesis, cut slightly obliquely.—E. Through the receptacle; several trunk bundles and two compound ventrals visible.—F. Bases of locules; compound ventral bundles formed.—G. Through lower part of locules, showing ovule traces departing from compound ventrals.—H. Through ovary; the compound ventral bundles dividing.—I. Through ovary; approaching top of the inferior portion; trunk bundles branching to form traces to stamens, phyllomes, and carpels.—J. Partial separation of the hypanthium from the ovary; insertion of some stamens and phyllomes; procambial strands of phyllome supply stippled here.—K. Carpels free of each other adaxially; hypanthium nearly free.—L. Insertion of remaining stamens and phyllomes.—M. Through the style bases, anthers, and phyllomes. (Key: A_3, tertiary axis; d, dorsal carpel bundle; lb, lateral branch; loc, locule; ov, ovule; phyl, phyllome; st, stamen, stamen trace; sty, style; tb, trunk bundle; v, ventral carpel bundle; vv, compound ventral bundle.)



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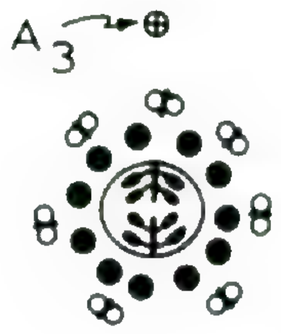

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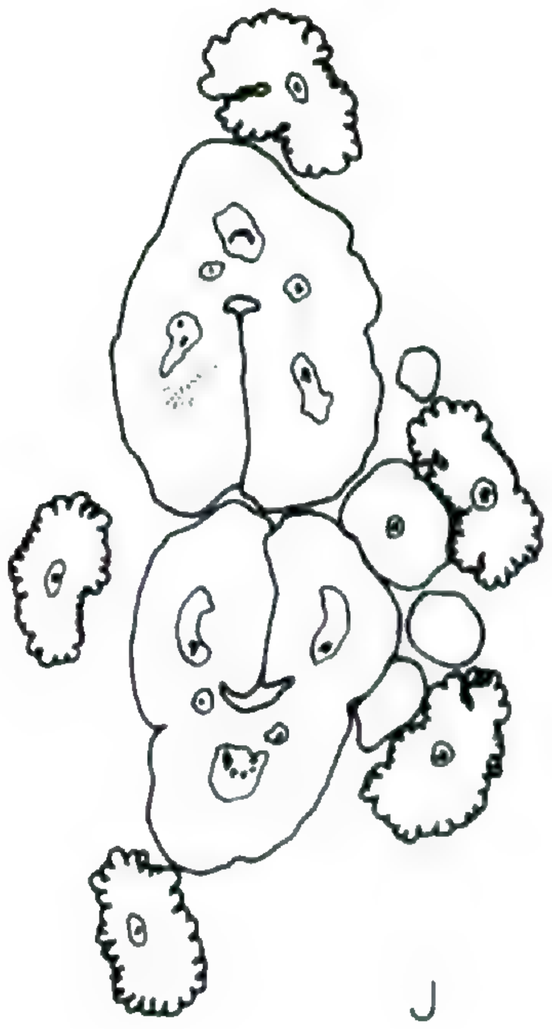

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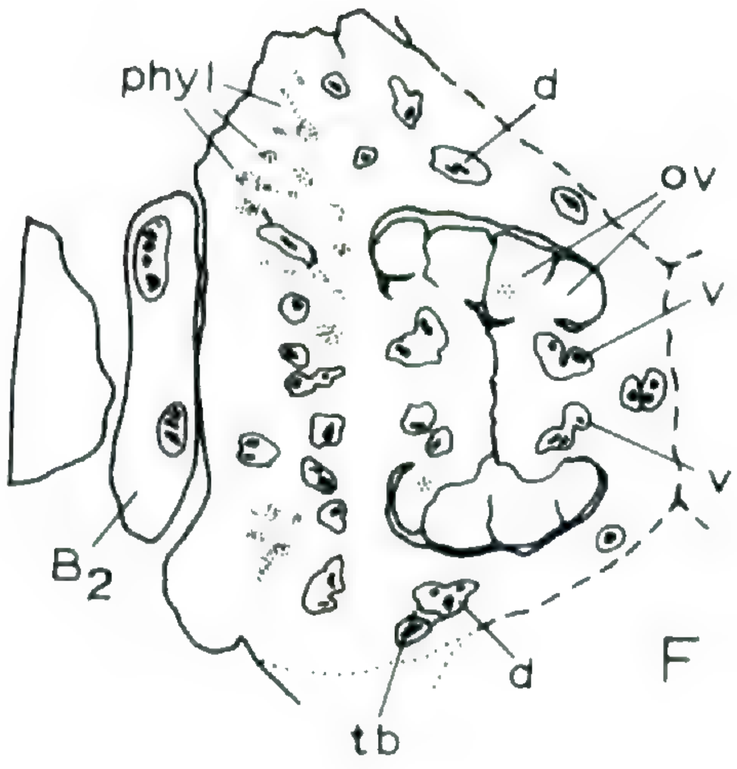

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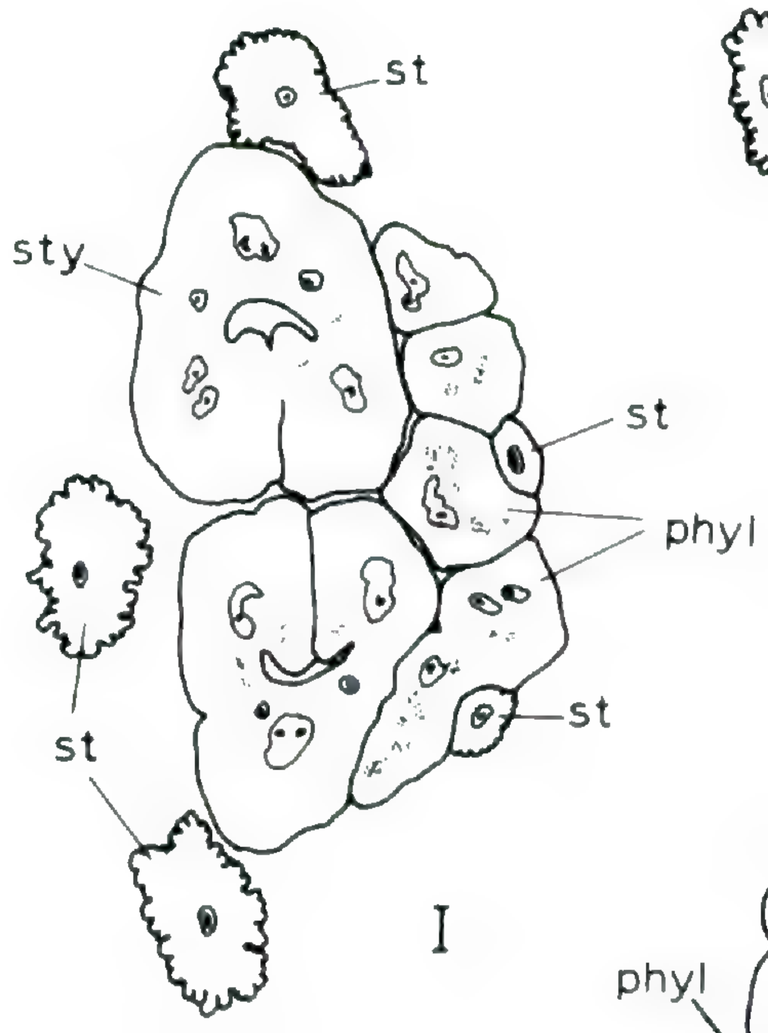

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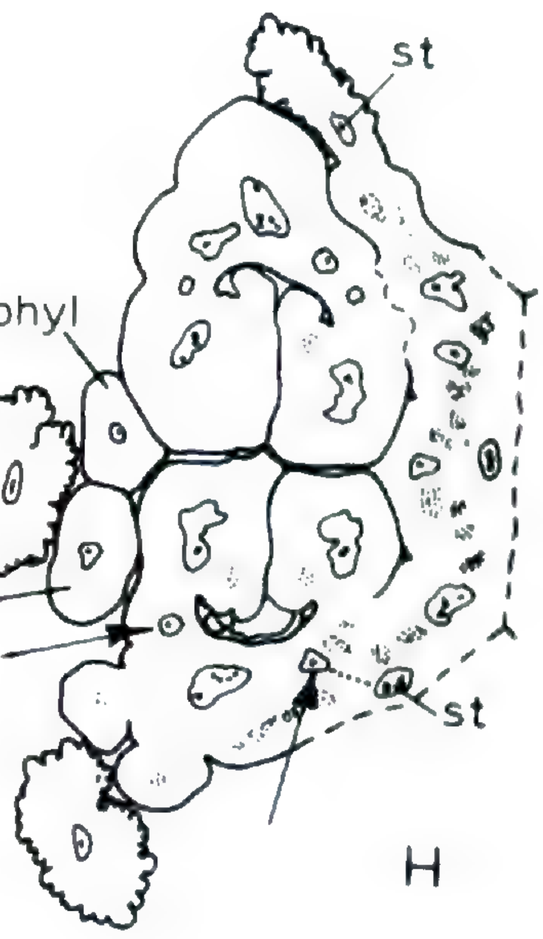

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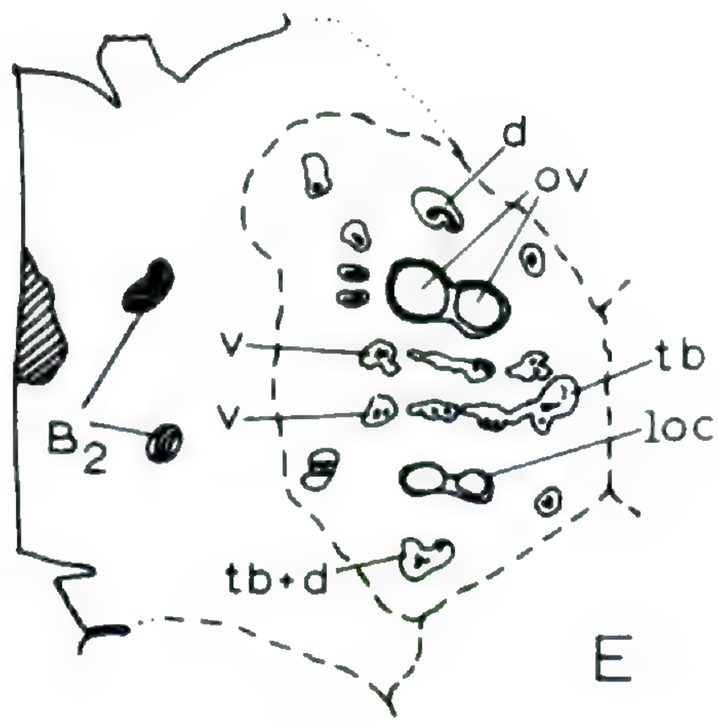

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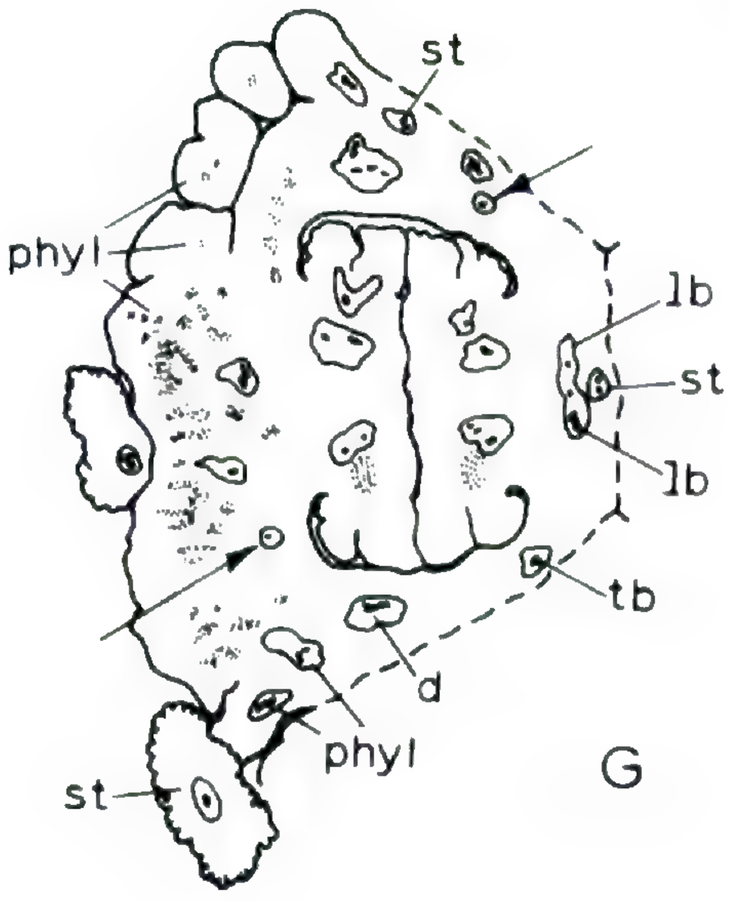

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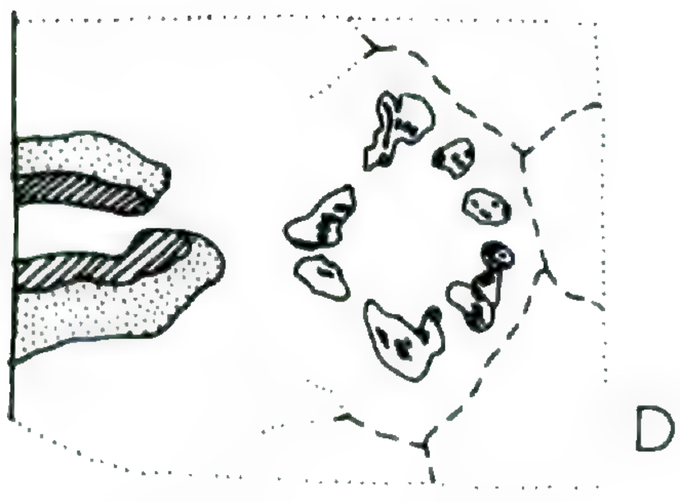

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entiated, unusual variations in inflorescence structure have frequently been observed and are also reported in the literature. On several occasions I have seen inflorescences of *Liquidambar styraciflua* and *L. orientalis* in which the flowers of the lower staminate heads contain partially developed but sterile gynoecia. Various degrees of development of the gynoecium among staminate flowers in a single head of *L. orientalis* are illustrated in Figure 4B, C. For the sake of clarity in these drawings the secondary bracts subtending the individual flowers or axillary floral clusters in the head have been removed (indicated by hatched areas), as have the anthers. In addition, each axillary group of flowers is illustrated in diagrammatic form to the left of the drawings. The secondary bracts are numbered in ascending order on the axis. Each stamen is represented in the diagrams by a small circle, a rudimentary ovary by an ellipse, and the absence of an ovary by a cross. Figure 4B(1) and 4E illustrate a single staminate flower consisting of seven stamens and lacking any external evidence of a vestigial ovary. This flower is seen in lateral view in Figure 4C(1), and diagrammatically in Figure 4E. Figure 4C(3) shows a secondary bract with a single, axillary, staminate flower that contains two rudimentary carpels surrounded by nine stamens (cf. diagram in Fig. 4F). The tips of the two abortive carpel primordia are apparent at either end of a minute pit in the center of the flower. Figure 4B(5) illustrates an axillary complex of seven staminate flowers of which five contain partially developed ovaries and styles, while two contain no ovaries. Although quite crowded on a short, conical axis, the limits of each flower could be ascertained by studying the placement and orientation of the stamens. Where two or three flowers abut, the stamens may occur in tufts of three or four. The composition of the seven flowers in the complex is shown diagrammatically in Figure 4D. The presence within a single staminate head of several secondary bracts with associated axillary floral clusters indicates clearly that each head of the inflorescence is a reduced branch system containing axes of at least two orders (secondary and tertiary) in addition to the floral pedicels and points up the complexity of the inflorescence in the subfamily.

Inflorescences of *Liquidambar styraciflua* in which all heads are developed to the pistillate state were reported by Britton (1887) and illustrated by Kirchheimer (1947). I have seen inflorescences in this condition on trees in the Arnold Arboretum and University of Washington Arboretum (Seattle), as well as on trees obtained from commercial sources and on native trees in eastern Pennsylvania. Such inflorescences are unusual but not rare and may be considered as concrete evidence of the bisexual potential of the staminate flowers of *Liquidambar*. Inflorescence variation of this type has also been observed in *Altingia*.

Although functionally pistillate, the female flowers normally contain stamens that are reduced and sterile. However, I have observed pistillate heads of *Liquidambar formosana* in which the stamens vary in development from tiny, clavate staminodia, as in Figure 2A, to fully developed stamens containing abundant pollen. The absence of a staining reaction with lactophenol–aniline blue, however, suggested that this pollen was not viable. Similarly, Shoemaker (1905) reported abortive pollen, and Schmitt (1965) reported viable pollen in the anthers of pistillate flowers of *L. styraciflua* in New York and North Carolina, respectively.

Floral vascular anatomy. In the following paragraphs the floral vasculature of *Liquidambar formosana* is first described in detail. The pat-

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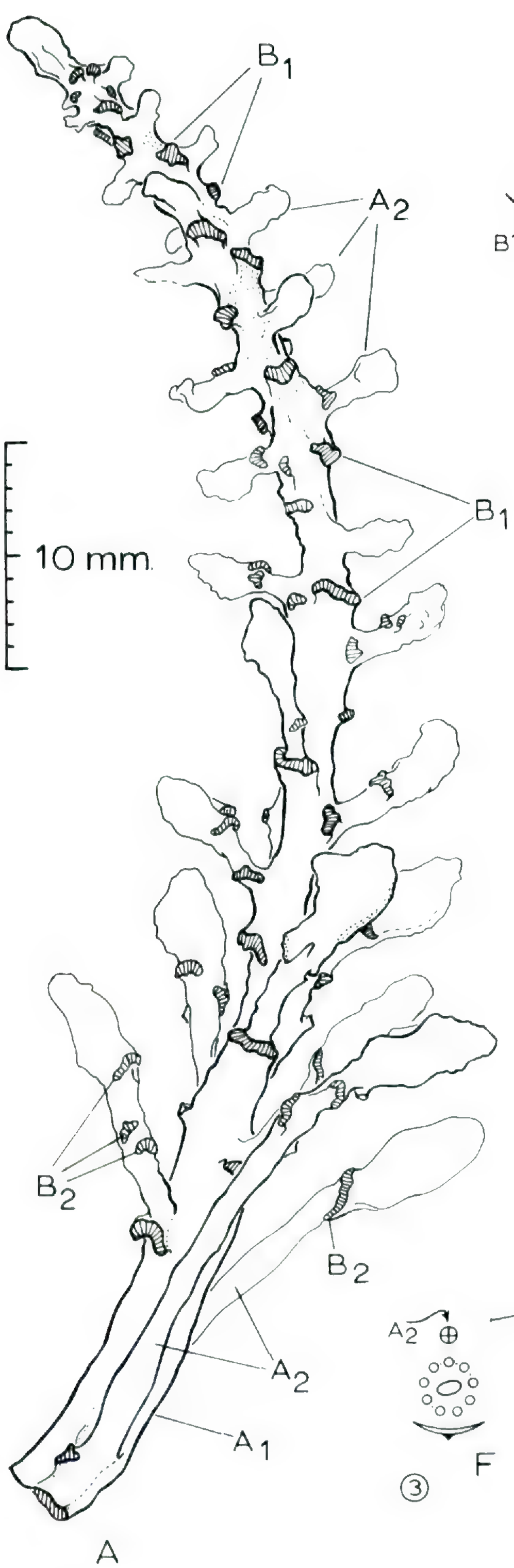
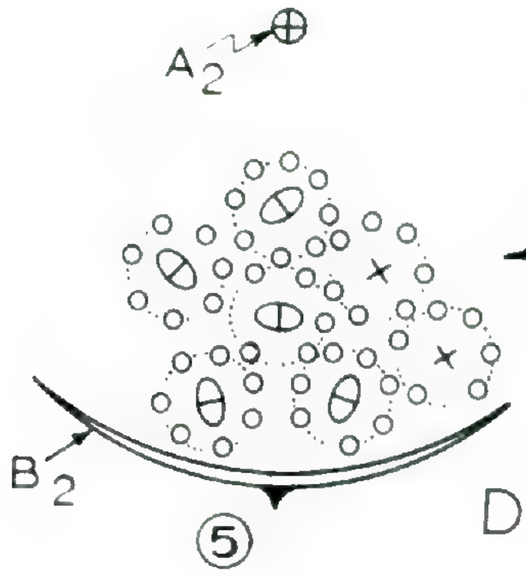
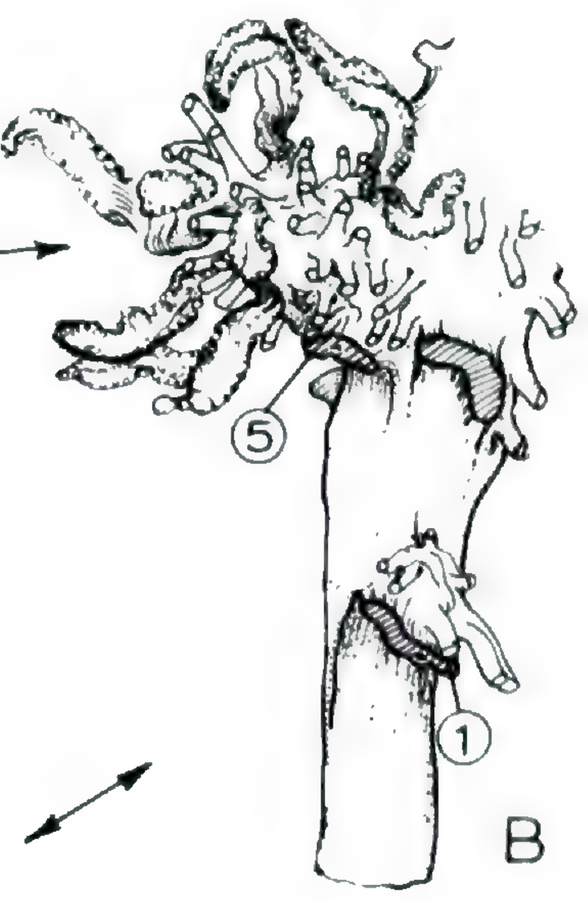
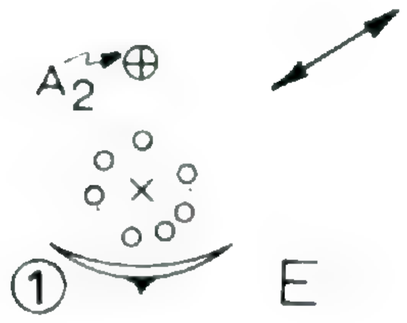
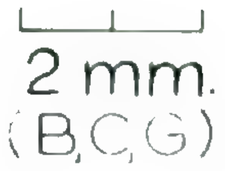
FIGURE 3. *Liquidambar styraciflua* L.—A. Pistillate flower at anthesis; one of the basal flowers in a head, with subtending secondary bract.—B. Floral diagram.—C. Stamen from a staminate flower. D–J. Serial sections of a pistillate flower at anthesis, cut slightly obliquely.—D. Through the receptacle, showing several large bundles.—E. Bases of locules; ventral bundles forming.—F. Through lower part of the ovary, showing branching trunk bundles on left; separation of placentae; traces to ovules departing from the ventral bundles.—G. Through the upper part of the inferior portion of the ovary; arrows indicate supplementary bundles to the carpel walls derived from trunk bundles.—H. Separation of the carpels; traces to stamens and phyllomes on the right side; procambial vasculature of the phyllomes stippled.—I. Insertion of the stamens and phyllomes on the right.—J. Through bases of styles, papillate anthers of sterile stamens. (Key: A_3, tertiary axis; B_2, secondary bract; d, dorsal carpel bundle; lb, lateral branch; loc, locule; ov, ovule; phyl, phyllome; st, stamen, stamen trace; sty, style; tb, trunk bundle; v, ventral carpel bundle.)

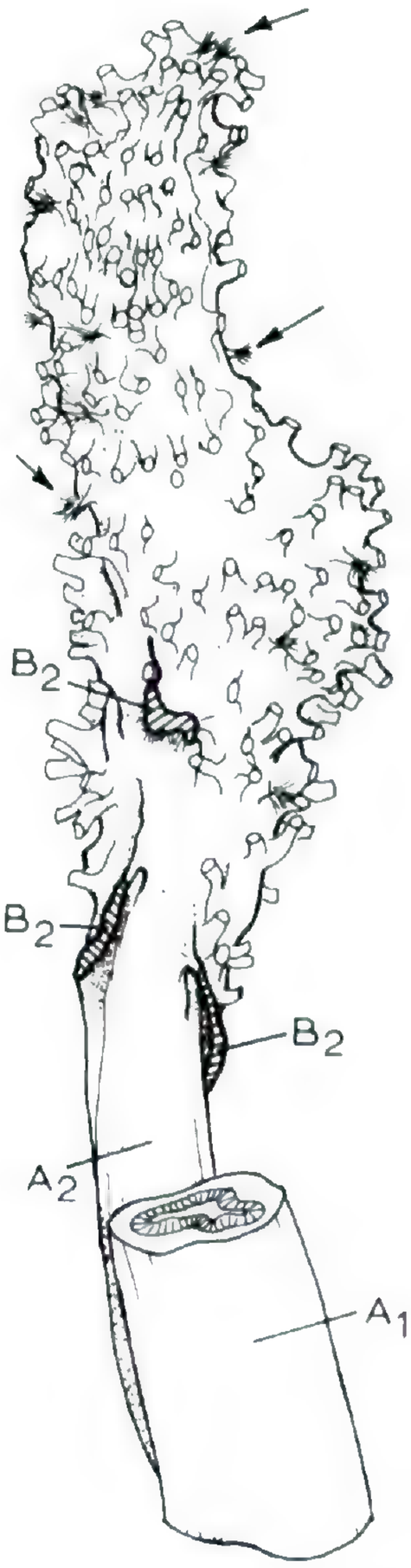












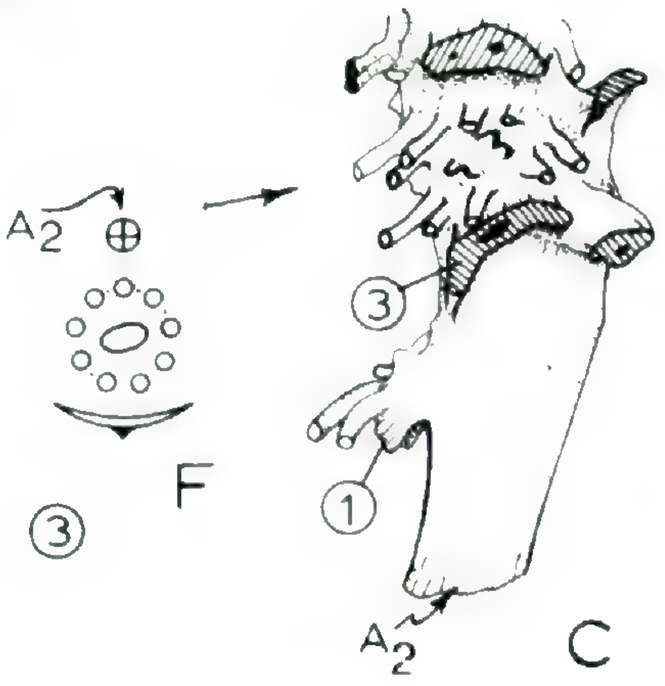


FIGURE 4. Staminate partial inflorescences of *Liquidambar styraciflua*, *L. orientalis*, and *Altingia chinensis*. — A. The staminate portion of the total inflorescence of *L. styraciflua* after anthesis, with all anthers removed, showing central primary axis with primary bract scars, and secondary axes with secondary bract scars. B, C. Portions of secondary axes of the staminate partial inflorescence of *L. orientalis*, showing various stages of

terns of the other two species are then described to the extent that they differ from that of *L. formosana.*

Pistillate flower. A typical pistillate flower of *Liquidambar formosana,* excised from a head, is illustrated in Figure 2A. At anthesis the major vascular features of the flower are discernible even though some of the vasculature is only procambial in those portions of the flower that later undergo considerable enlargement and development (e.g., the ramifying bundle systems in the cycle of phyllomes, or the vascular network of the carpel walls).

The vascular supply to the flower is variable. As many as ten bundles enter the base of the sessile flower from the peduncular stele (Fig. 2E). In the receptacle these rapidly give rise to a peripheral system of five to eight trunk bundles (tb), which eventually supply the stamens, the phyllomes, and the carpels as an inner series of four ventral (v) and two dorsal (d) carpel bundles (Figs. 2F–H, 6I). There is also considerable variation in the organization of the dorsal and ventral bundles. A dorsal bundle may be formed in the ovary wall by the radial or tangential division of a trunk bundle; through the fusion of two lateral branches from adjacent trunk bundles; or directly by one of the bundles entering the receptacle from the peduncular stele. Except in the last case the formation of the dorsals occurs at varying levels in different carpels.

The ventral bundles originate from the receptacle below the base of the locules. The ventrals of adjacent fused carpel margins may originate individually as branches from trunk bundles, or they may be united in a compound ventral bundle (vv) in the base of the ovary (Fig. 2E, F). If united basally, the individual ventrals (v) become distinct in the septum a short distance above the bases of the locules (Fig. 2G, H).

The peripheral trunk bundles (tb) ascend in the wall of the hypanthium to supply the stamens and phyllomes. At the base of the androecium each trunk bundle branches tangentially. The abaxial branch supplies a single trace (st) to the base of a sterile stamen (Fig. 2H–J). The adaxial branch then divides to form two to three branch traces (phyl), which supply the bases of adjacent phyllomes. If a single large phyllome occupies the position between two adjacent trunk bundles (or sterile stamens), its base may receive traces from each of the adjacent trunk bundles. If two smaller phyllomes occur between two trunk bundles, each will receive one or more traces from each of the nearest trunk bundles. The traces ramify extensively in the fleshy base of the phyllome, forming an ascending system of bundles (indicated by stippling in Fig. 2J, K). At higher levels in the phyllome only a single prominent central bundle persists (Fig. 2K, L), ascending to the tip of the phyllome, as has been noted also by Schmitt (1965). In transverse sections the bases of the phyllomes often appear lobed and divided (Fig. 2J, K), and the larger lobes, at least, may be supplied by procambial strands at anthesis. The secretory ducts that accompany the vascular bundles throughout the plant are also present in the bundle systems of the phyllomes. At the level of separation of the carpels from the phyllomes (Fig. 2J–L), it often appears that the stamen and phyllome bases remain fused for a very short distance, as if in a floral tube. This may or may not represent the vestige of a hypanthial tube. This condition is occasionally present in *Liquidambar styraciflua* as well.

The dorsal carpel bundles pass upward and, in the apocarpous portion of each carpel, produce at least two pairs of subopposite secondary branches that move upward and toward the carpel margins, where they fuse with the ventral bundles. Transverse sections may thus show four to seven bundles in the carpel wall (Fig. 2L, M).

The ventral carpel bundles (vv, v) ascend through the septum and into the placentae (Fig. 2F, H, I). Traces to the ovules are produced in both the septum (Fig. 2G) and in the free com-

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gynoecial development in staminate flowers.—B. Secondary bract (5), with axillary complex of seven flowers, several of which contain partially developed gynoecia. Compare with the diagrammatic presentation at D. Secondary bract (1), with a single axillary flower with seven stamens, no gynoecium. Compare with diagram at E.—C. Secondary bract (3), with a single axillary flower containing eight stamens and two abortive carpel primordia at either end of a central depression (stippled). Compare with diagram at F.—D–F. Diagrammatic representations of the flowers illustrated at B and C.—G. The clavate secondary axis of a single staminate head from an inflorescence of *Altingia chinensis.* Pubescent vestigial carpel primordia indicated by arrows. (Key: A_1, primary axis; A_2, secondary axis; B_1, primary bract; B_2, secondary bract; circled numerals designate bracts and associated axillary flowers.)

pound placentae (Fig. 2H, I); placentation is thus axile below, but parietal above. In the distal portion of the ovary the ventrals produce an occasional minor branch to the carpel wall before passing into the style bases.

The vascular anatomy of the female flowers of *Liquidambar orientalis* and *L. styraciflua* (Fig. 3) is essentially like that of *L. formosana.* The origins of the dorsal and ventral bundles of the ovaries of these species are fully as variable as in *L. formosana* (cf. Fig. 3D–F). An interesting deviation, however, is the adnation in these two species of a lower pair of carpel secondary veins to nearby trunk bundles of the hypanthium. Each of these secondary bundles originates below the level of separation of carpel from hypanthium, arising as a branch from a trunk bundle (or one of its major branches) on either side of the dorsal bundle (arrows, Figs. 3G, H, 6D). They move adaxially into the carpel wall and eventually fuse with adjacent ventral bundles.

In *Liquidambar styraciflua* (*Bogle 823*) the ventral bundles may appear slightly diffuse (Fig. 6A, B), with some of the strands diverging to form ovule traces while others ascend into the style bases. In other cases the ovules may be supplied from a branch of the ventral that dies out after supplying traces to the ovules.

The ramifying bundle system that vascularizes phyllomes, as seen in cleared specimens of *Liquidambar styraciflua,* varies from quite complex (Fig. 6C, *Bogle 823*) to relatively simple (Fig. 6D, *Bogle 790*). In scanning electron micrographs widely scattered stomata can be seen in the epidermis of both the phyllomes and carpels of *L. styraciflua.*

Staminate flower. Typical staminate flowers in all three species are highly modified (Fig. 4B, C), and the vasculature of their receptacles and axes is very diffuse and complex. In cleared staminate heads individual flowers are barely or not at all discernible on the basis of vasculature alone. Stamen bundles radiate from the margins of gaps in a loosely expanded peduncular stele. Each gap appears to correspond to a single flower, but gaps may become confluent, forming large open spaces in the stele. A bundle emanating from the margin of a gap may: supply a single stamen base directly; divide to form two traces to separate stamens; or anastomose with a second bundle to form the supply to one stamen. I found no evidence of a vascular supply to any of the abortive carpel primordia mentioned above and illustrated in Figure 4. But it would not be surprising to find such a supply in staminate flowers with partially developed gynoecia, such as those of *Liquidambar orientalis* illustrated and diagrammed in Figure 4B(5) and 4D.

2. Altingia Noronha, Verh. Batav. Genootsch. Kunsten 5(2): 1. 1790. Figures 1B, 4G, 5, 6E–J.

About seven to 14 species are currently recognized in the genus *Altingia* (Vink, 1957; Tardieu-Blot, 1965; H. T. Chang, 1962, 1973, 1979). The genus is distributed from Bhutan and Assam eastward to southern China, and southward through Malaya to Java and Sumatra. In their natural state the massive, evergreen trees of *Altingia* may achieve heights of up to 60 meters, prompting their description as the kings of the mountain forests in southeast Asia, particularly in Indonesia.

The evergreen leaves of *Altingia* are simple to pinnately-lobed, stipulate, with an entire or serrate margin. They contrast sharply in form with the deciduous, palmately-lobed and -veined leaves of *Liquidambar.* However, intermediate leaf forms, and conditions of persistence, are described in the species attributed to the segregate genus *Semiliquidambar* H. T. Chang (1962, including *A. chingii* Metc. as *Semiliquidambar chingii,* and four new species, since reduced to three by H. T. Chang, 1979).

Morphology. Inflorescences of *Altingia* are terminal on vegetative axes, and appear to be basically similar to those of *Liquidambar* in composition, with a comparable range of variation. The staminate heads are often more elongate and oblong in appearance than those of *Liquidambar* (Fig. 1), and the internodes and peduncles are often longer, giving the total inflorescence a longer, looser appearance. The majority of herbarium specimens seen bear only older pistillate heads; very few bear anthesis stage or young inflorescences that permit observations of the total inflorescence. This problem is noted by Tardieu-Blot (1965) in her treatment of the six species of *Altingia* occurring in Cambodia, Laos, and Vietnam. In fact, flowers are listed as unknown for five of the six species she describes. Vink (1957) described the inflorescences of Malaysian *Altingia* in part as: "male heads in racemes consisting of masses of stamens, intermingled with some minute ?bracts," and "female heads solitary, in racemes or in the lower part of male racemes."

Young inflorescences containing at least one

pistillate head at the basal node, with numerous distal nodes bearing pedunculate to sessile staminate heads, have been observed in herbarium specimens (GH, A) of *Altingia chinensis* (Champ.) Oliver, *A. excelsa* Nor., *A. gracilipes,* and *A. obovata* Merr. & Chun. Some inflorescences of *A. chinensis* have two or three pistillate heads at the basal nodes. In contrast, unisexual inflorescences of *A. excelsa* containing 11–16 pistillate heads arranged in a narrowly conical fashion occur in specimens of *Abbe 10298* in my collections. In these, the lower heads are pedunculate, the intermediate and upper heads grade from short-pedunculate to sessile, whereas the two or three most distal heads are fused in a terminal mass.

The number of flowers in each pistillate head varies among the species of *Altingia* from numerous (in excess of 25) to as few as six. In fruit this results in heads that range in shape from globose in species such as *A. chinensis* or *A. yunnanensis,* to obovate or obpyramidal in *A. takhtajanensis* and *A. siamensis* (compare illustrations in Tardieu-Blot, 1965, pl. IV, V). This contrasts with the many-flowered pistillate heads of *Liquidambar,* which are typically globose.

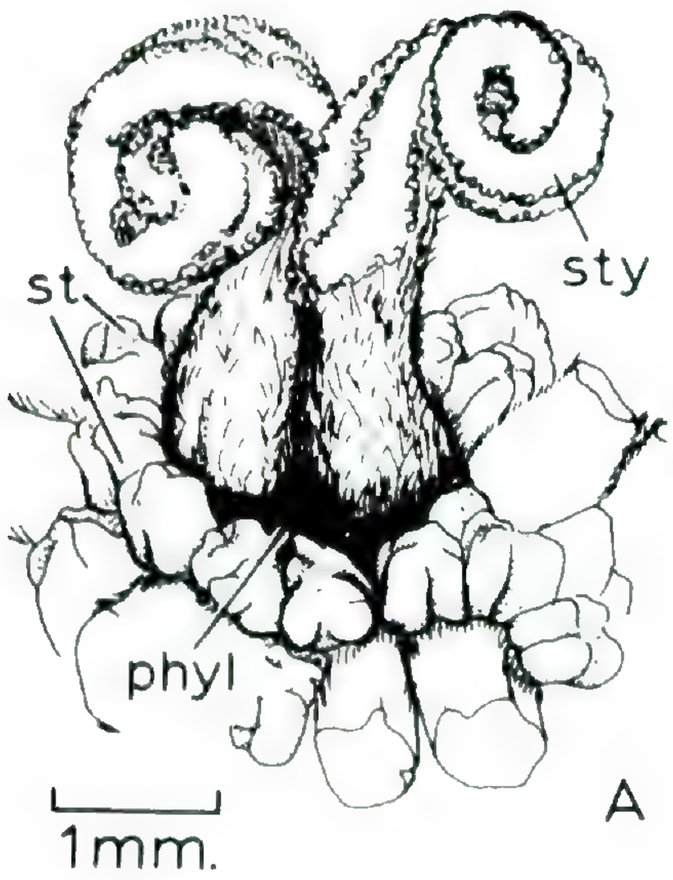
Pistillate flower. As in *Liquidambar,* I found no morphological evidence of a calyx or corolla (Fig. 5A, B). On the surface of the pistillate head three to ten stamens define the periphery of each flower. Their anthers are often rudimentary and misshapen, but in some cases they are fully formed and contain abundant pollen. The anthers are broadest abaxially, and the connective is frequently minutely apiculate adaxially (Fig. 5A). Stamens in which the anther connectives are elaborated into stylodia with stigmatic surfaces (Fig. 6F–H) have been observed in one specimen of *A. chinensis* (*Pételot 5944,* A). A cycle of short, inconspicuous, pubescent phyllomes occurs between the stamens and style bases (Fig. 5M). In maturing flowers the phyllomes appear broader and more massive, with more complex lobing than those in *Liquidambar.* The apocarpous portions of the two carpels are short, thick, and pubescent. Within the half-inferior ovary a shallow partial septum divides the base of the locule, but shortly gives way to two appressed parietal placentae (Fig. 5E, F). A count of the number of ovules per carpel margin in specimens at hand showed 12–16 (28–31 per carpel) in *Altingia chinensis* (*Pételot 5944,* A) to 20–25 (41–47 per carpel) in *A. excelsa* (*Bogle 583*). The ovules are anatropous and become angular to weakly winged at maturity.

The form of the sterile phyllomes varies among the species of *Altingia.* In most species these organs are short, broad, blunt, and pubescent structures (Fig. 5A, M). In a specimen of "*A. chinense*" from Tonkin (*Pételot 5944,* A), however, I observed subulate phyllomes (Fig. 6E) comparable to those of *Liquidambar formosana,* and similar subulate organs 4–6 mm long are described by H. T. Chang (1962, as "calyx limb") in *Semiliquidambar cathayensis* H. T. Chang (*A. chingii* Metc. pro parte).

Staminate flower. The staminate flowers of both *Altingia chinensis* and *A. excelsa* are also similar to those of *Liquidambar.* The pedunculate secondary axis of a staminate head of *A. chinensis,* from which all the anthers have been removed, is illustrated in Figure 4G. The individual flowers are indistinct, having merged with the axis. In undistorted flowers a single cycle of stamens is inserted around the periphery of a shallow depression in the surface of the axis. The anthers are tetrasporangiate, with a broad, fleshy cap formed by the connective (Fig. 5C). The surface of the depression is very finely and minutely pubescent, catching many pollen grains. At either end of the depression the tip of an abortive carpel primordium is often evident. Each tip bears a tuft of hairs (Fig. 4G, arrows). The scars of three secondary bracts (B_2) are also apparent on the surface of this axis. Each secondary bract subtends a group of staminate flowers, the lowest of which are greatly distorted. The axis of this head thus represents at least three axillary floral clusters fused into a common mass. This morphological evidence suggests that the partial inflorescences of *Altingia* represent condensed branch systems comparable to those described for *Liquidambar styraciflua* by Wisniewski and Bogle (1982). However, similar studies in *Altingia* are needed.

Floral vascular anatomy. The principal basis for comparison with *Liquidambar* used here is the vascular anatomy of the functionally pistillate flowers. The vasculature of the staminate flowers is greatly reduced, modified and irregular, as in *Liquidambar,* and no attempt is made to describe it here.

Pistillate flower. Reduction of the peduncular and pedicellar axes in the pistillate heads in *Altingia* appears more advanced than that in *Liquidambar,* resulting in increased congestion of the flowers. The peduncular stele is expanded into a loose network of branching and anastomosing bundles, and the abbreviated, loosely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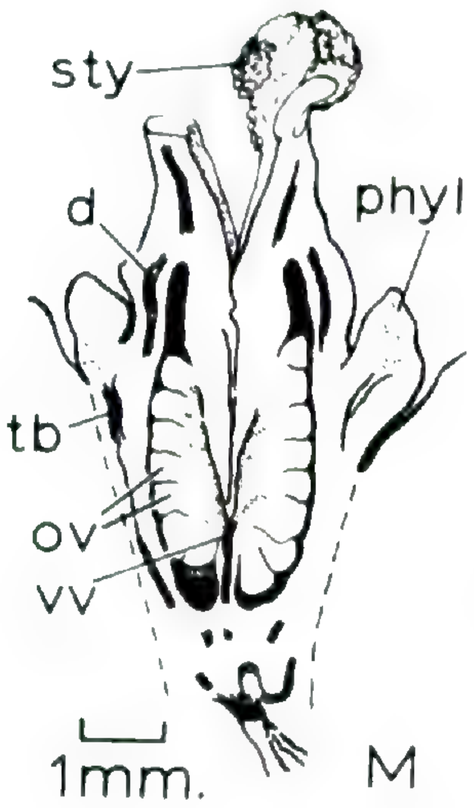
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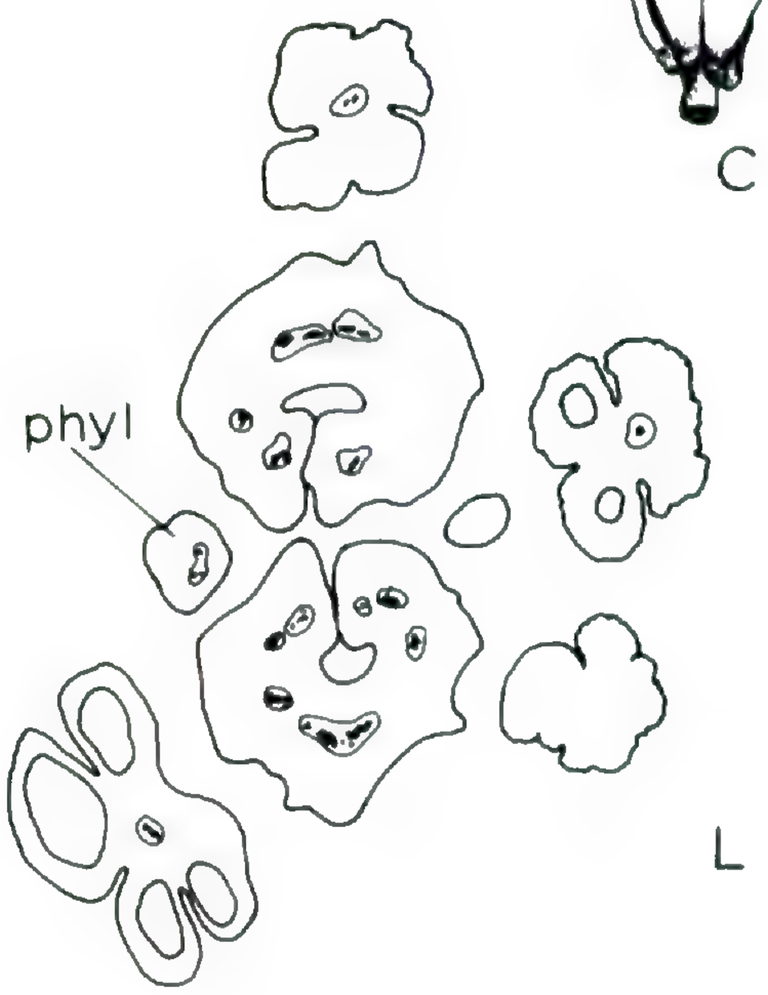
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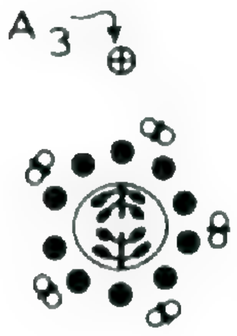
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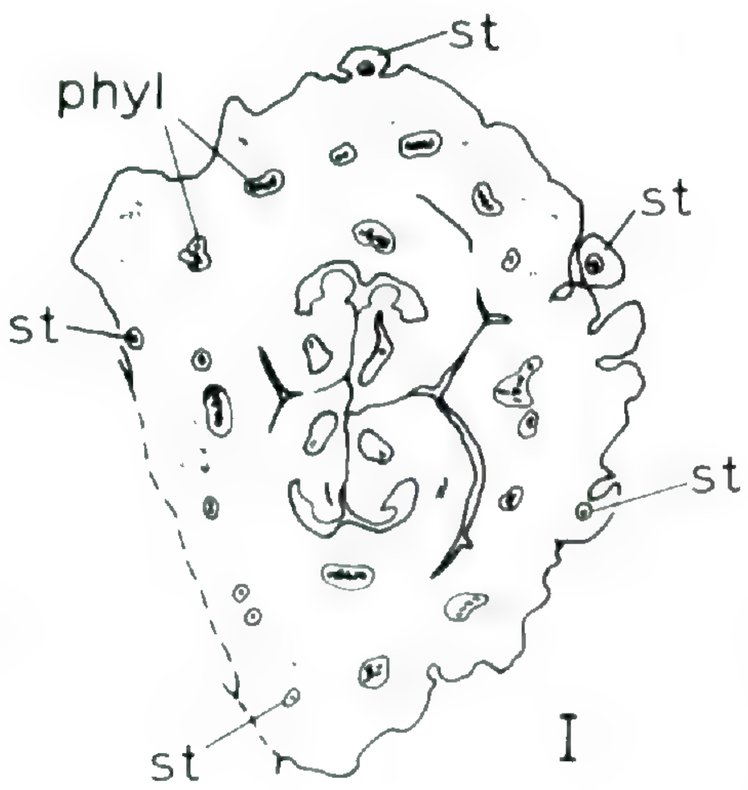
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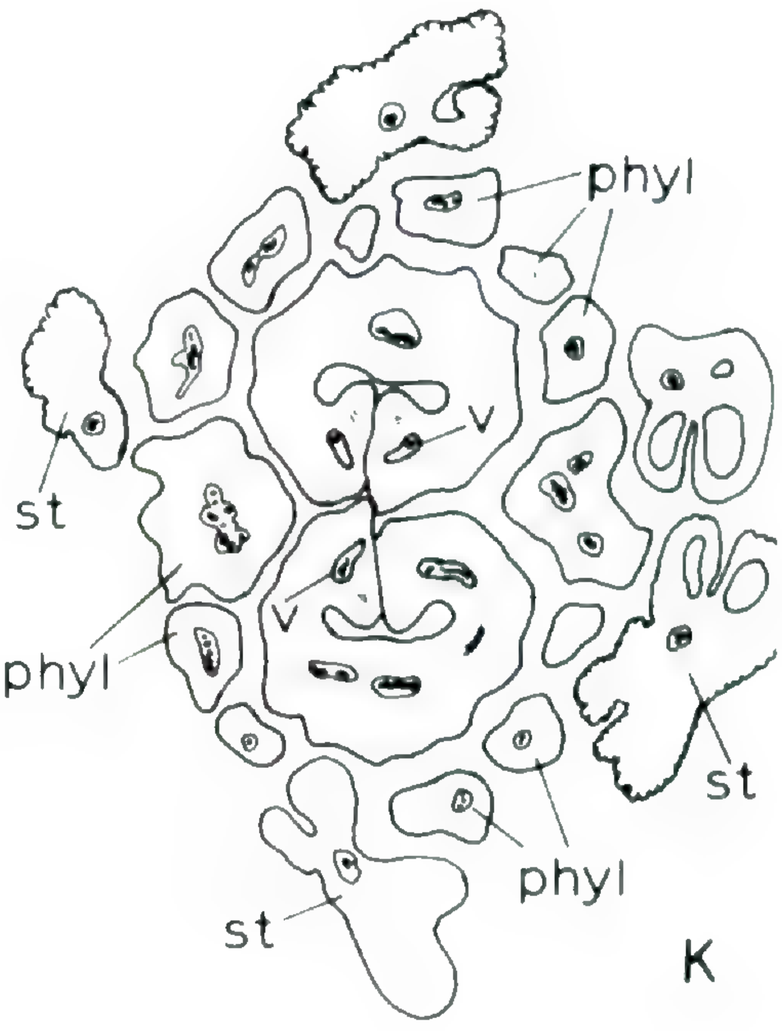
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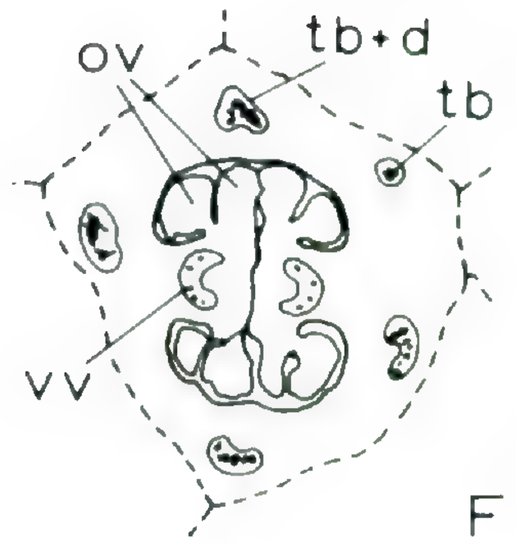
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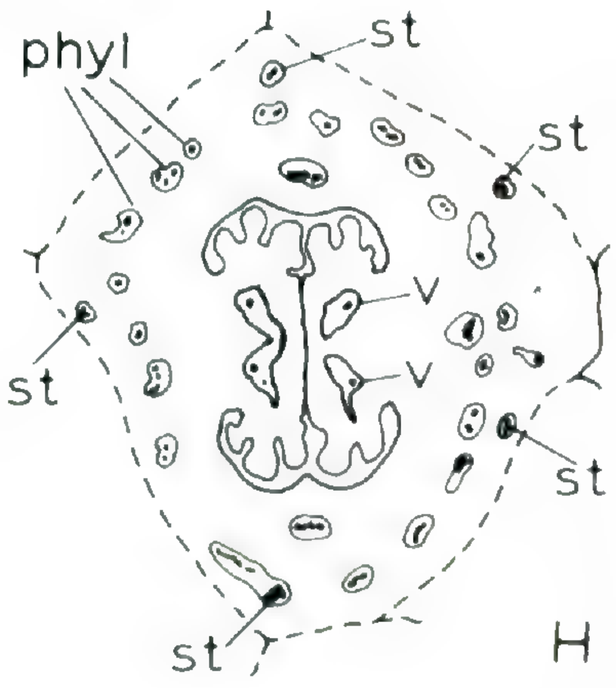
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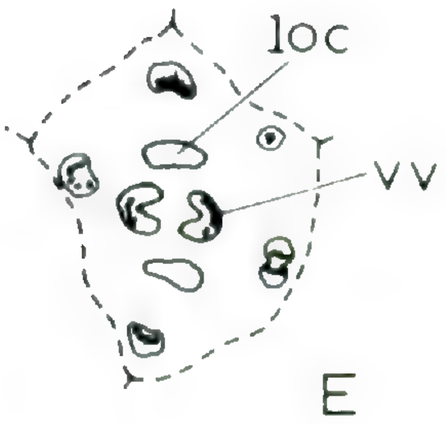
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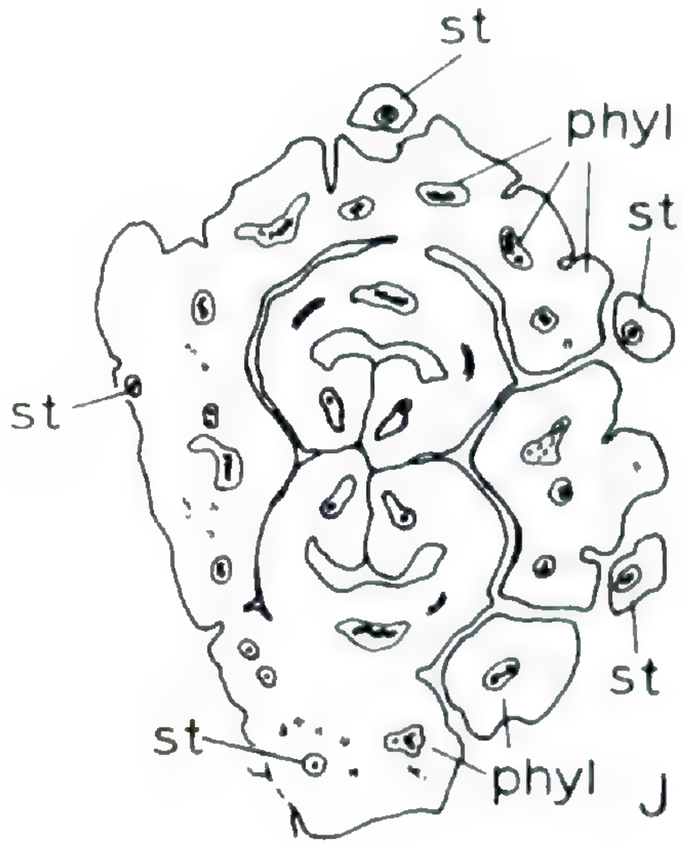
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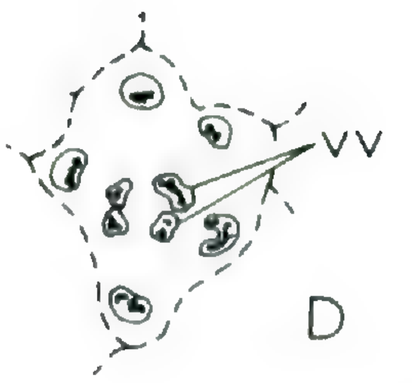
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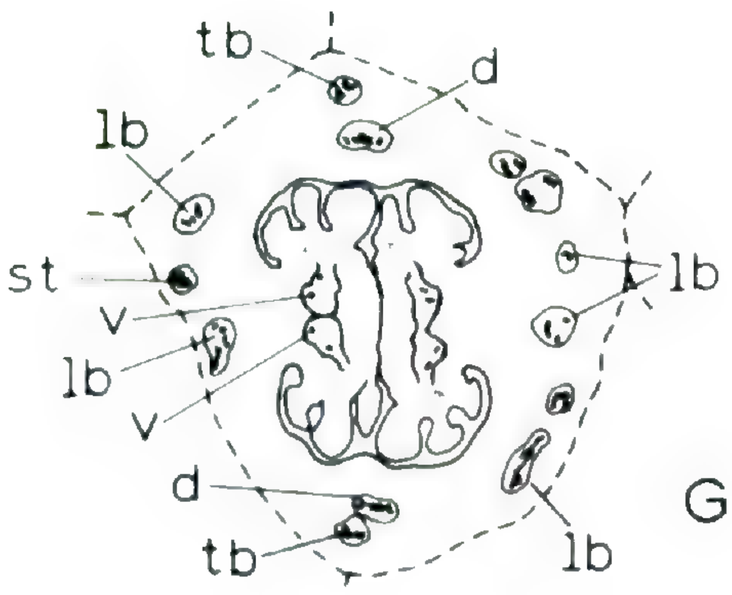
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1 mm.

formed pedicellar cylinders seen in the receptacles of pistillate flowers of *Liquidambar* are absent here. An indication of the increased reduction and fusion within the heads is the occurrence of basal fusions between the trunk bundles of adjacent flowers. These bundles separate to their appropriate flowers at a relatively low level. Such fusions were not noted in the species of *Liquidambar*.

Several (five to seven) vascular bundles diverge directly from a gap in the peduncular stele into the relatively broad base of the sessile flower (Fig. 5D). These bundles may function simply as hypanthial trunk bundles, supplying traces to the stamens and the sterile phyllomes (fleshy, sterile "disk" lobes of Vink, 1957), or they may divide to supply dorsal or ventral bundles to the gynoecium as well. The number of trunk bundles corresponds to the number of stamens in most cases (Fig. 5E, F). As the trunk bundles ascend in the hypanthium they begin to branch at a level slightly below the separation between the carpels and the phyllomes (Fig. 5G). Each trunk bundle usually produces a trace (st) to a rudimentary stamen, as well as lateral branches (lb) to one or both sides. The latter may function directly in supplying the base of a phyllome or may anastomose with a lateral branch from an adjacent trunk bundle to form such a supply. Each major lobe of the cycle of phyllomes is thus supplied with a vascular bundle. Within the lobe the bundle ramifies to form a complex system of minor bundles, procambial at anthesis, many of which terminate in small protrusions on the abaxial side of each lobe (Fig. 5H–J).

At the level of separation of the carpels from the phyllomes the stamen and phyllome bases may appear fused for a short distance, as if in the rim of a hypanthial tube (Fig. 5I, J).

The formation of the carpel ventral bundles is variable. They are formed immediately in the base of the flower, frequently before either dorsal bundle is evident. One to three vascular strands become associated at either side of the receptacle in the transverse plane to form a compound ventral bundle (vv in Figs. 5D, E, 6J). In some serial sections, and in some cleared flowers, the compound ventral bundles appear to consist of a central strand flanked on either side by minor lateral strands that diverge slightly, giving the impression of a second bundle in each carpel margin. In cleared material these divergent bundles are seen to persist for only about a third of the length of the ovary. In serial sections they are seen to dissipate in procambial strands to the lowest inserted ovules. They appear to represent minor placental strands of the ventral bundles, rather than a second bundle in each margin. A similar situation is seen in *Liquidambar styraciflua* (Fig. 6A, B).

At the level of insertion of the lowest ovules the compound ventral bundles (vv) divide, forming individual ventral bundles (v) to each of the adjacent fused carpel margins (Fig. 5G). Above this level the traces to the ovules originate from the free ventral bundles (Fig. 5H), which finally pass unbranched into the styles (Figs. 5J, 6J).

The carpel dorsal bundles (d) may be distinct at the base of the locules, but more often they are fused basally with one or more of the peripheral trunk bundles and do not separate until about halfway up through the inferior portion of the ovary (Fig. 5G).

Secondary carpel wall bundles appear only as the hypanthium begins to separate from the ovary. Above this level (Fig. 5I–L), lateral branch bundles pass directly from dorsal to ventral bundles, often almost horizontally. Each lateral is accompanied by a gum duct, as are the dorsal and ventral bundles. There is no evidence in my material

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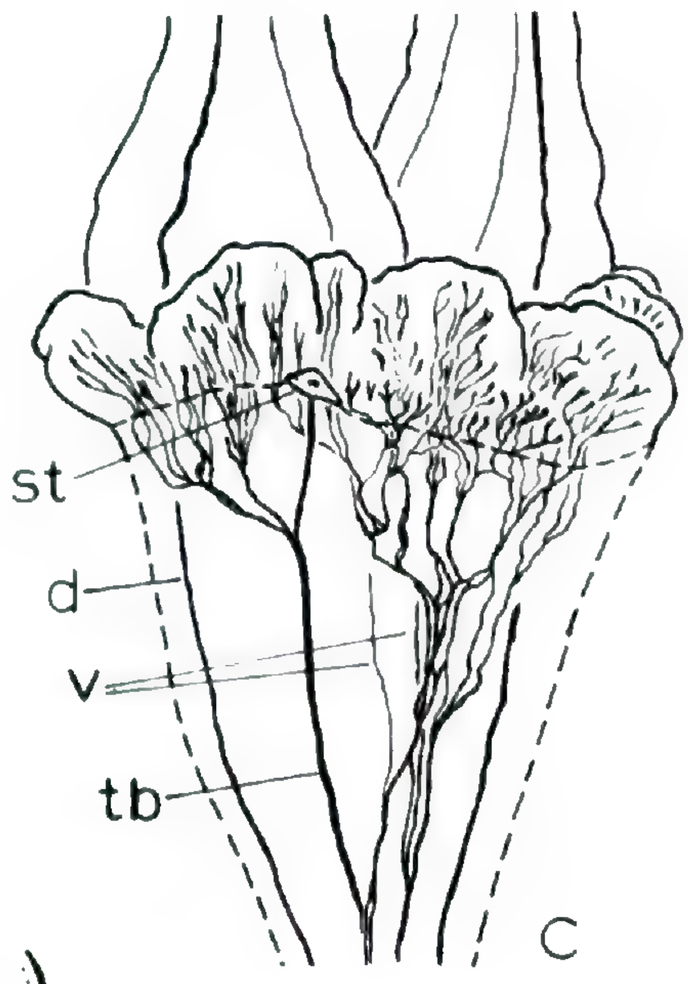
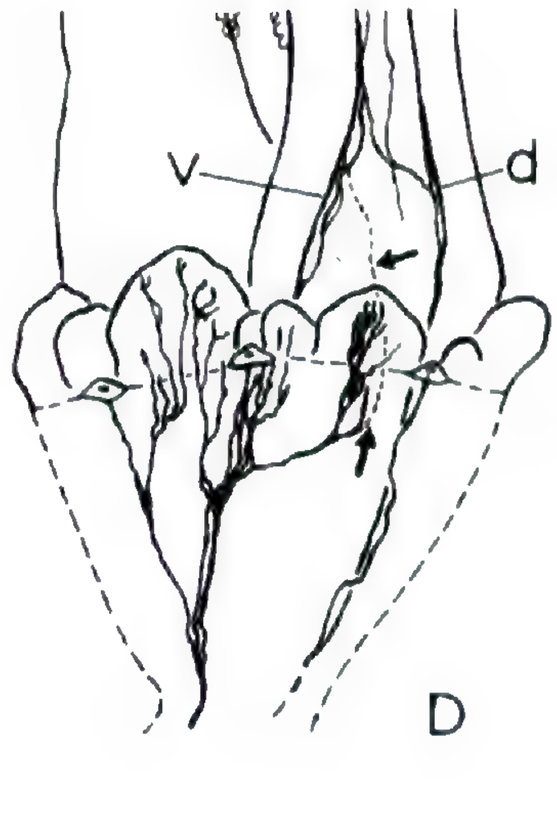
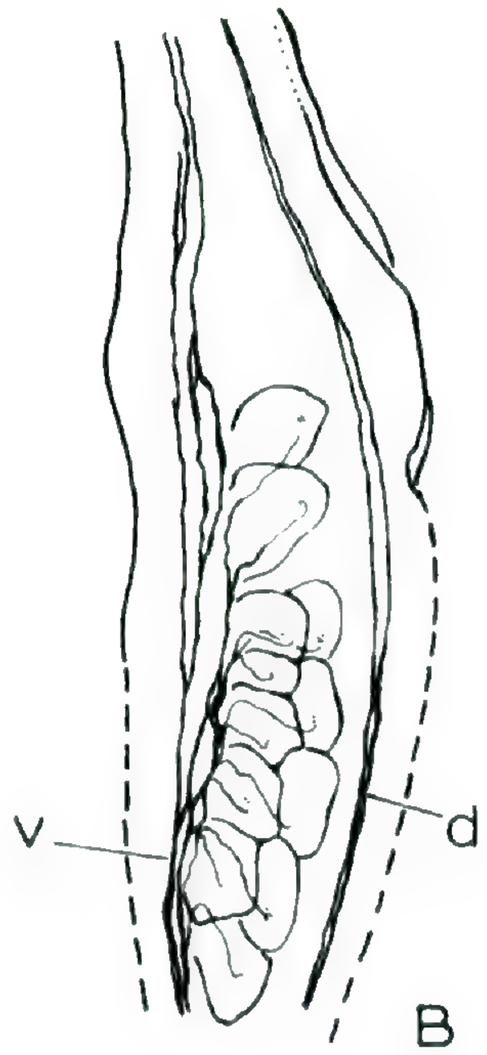
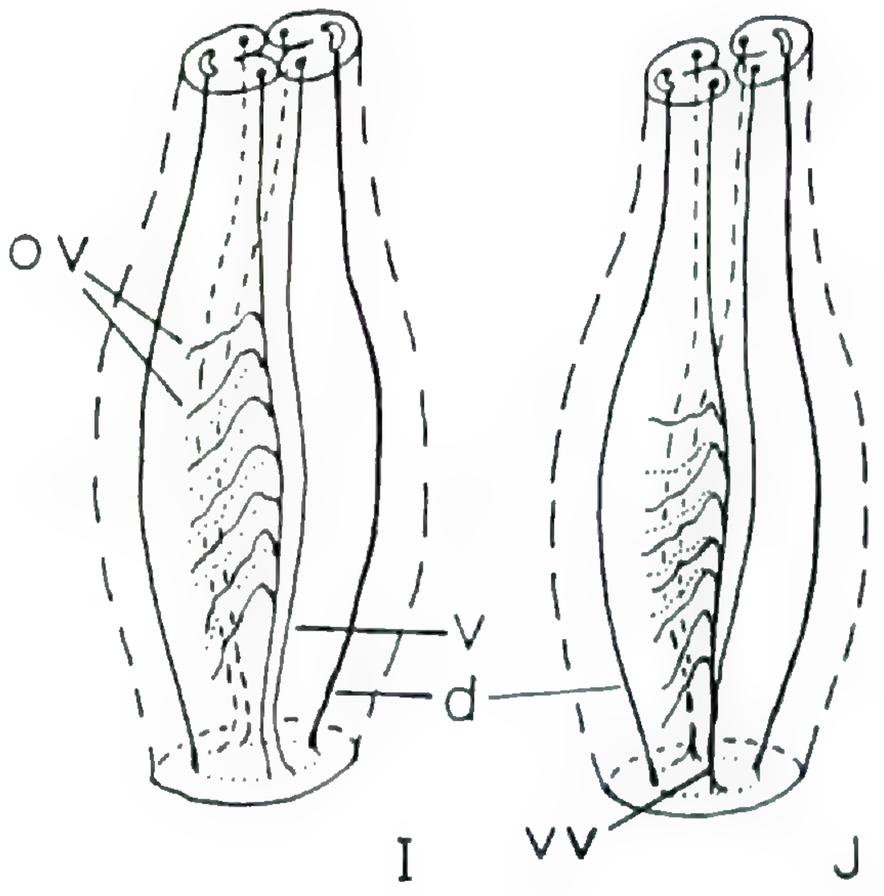
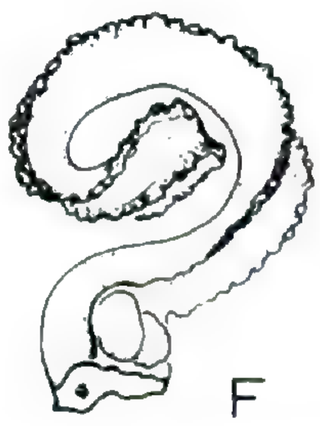
FIGURE 5. *Altingia excelsa* Nor.—A. Pistillate flower at anthesis. Parts of adjacent flowers shown.—B. Floral diagram.—C. Stamen from a staminate flower. D–L. Serial sections of a pistillate flower at anthesis.—D. Receptacle; several peripheral trunk bundles and compound ventral bundles evident.—E. Bases of locules.—F. Slightly above the locule bases, showing separation of the parietal placentae.—G. About mid-height in inferior portion of ovary, showing dividing compound ventral bundles, branching trunk bundles, ovular traces departing from ventral bundles.—H. Through upper part of inferior portion of the ovary; stamen traces and ramifying bundles to the phyllomes shown.—I. Partial separation of the hypanthium from the carpels, and of the carpels from each other.—J. Insertion of the stamens and phyllomes.—K, L. Sections through the style bases, showing phyllomes and anthers of the sterile stamens.—M. Drawing made from a longitudinal hand section through a pistillate flower in the median plane, showing numerous ovules, insertion of phyllomes. (Key: A_1, primary axis; A_2, secondary axis; d, dorsal carpel bundle; lb, lateral branch; loc, locule; ov, ovule; phyl, phyllome; st, stamen, stamen trace; sty, style; tb, trunk bundle; v, ventral carpel bundle; vv, compound ventral bundle.)

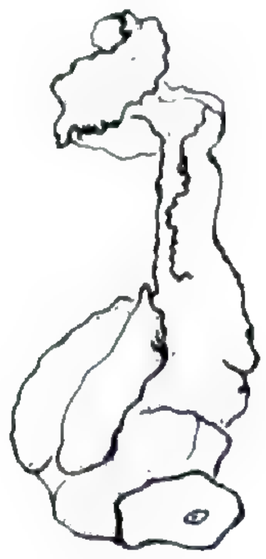












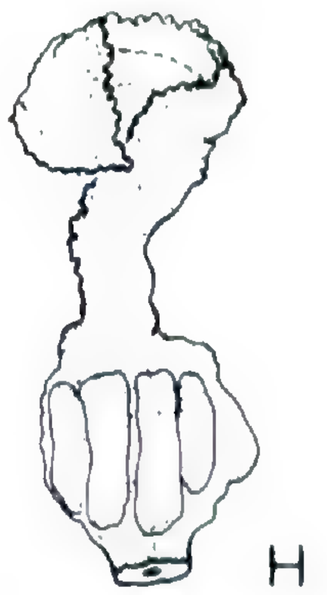


FIGURE 6. A–D. *Liquidambar styraciflua*.—A. Vasculature of gynoecium of the pistillate flower, showing dorsal and ventral carpel bundles, and the ovule traces originating from the ventral bundles on the near side (*Bogle 823*).—B. Vasculature of one carpel enlarged, showing dorsal bundle and ventral bundle of near margin with ovule traces; ovules outlined (*Bogle 823*).—C. Ramifying vascular supply to phyllomes of the pistillate flower; one stamen trace and insertion scar indicated. Note that one dendritic system supplies branches to more than one lobe of the cycle of phyllomes in both C and D (*Bogle 823*).—D. Less elaborate vascular supply to phyllomes of a pistillate flower (*Bogle 790*). E–H. *Altingia chinensis* (*Pételot 5944*).—E. Pistillate flower with one stylodeus stamen with half-anther (stl), one scale-like staminodeum with half-anther (sto) and numerous

of vascular bundles contributed to the carpel walls by the hypanthial bundles, as in *Liquidambar orientalis* and *L. styraciflua*.

Discussion

The taxa of subfamily Liquidambaroideae exhibit an interesting combination of relatively primitive and advanced morphological and anatomical characteristics. The complex inflorescences are terminal on long or short vegetative axes. Subsequent vegetative growth develops from axillary buds.

Morphological evidence from mature inflorescences indicates that the total inflorescence in the subfamily is derived from a compound raceme by reduction, and that a minimum of three orders of axes (or four if the floral pedicels are taken into account) are present. Ontogenetic study of the total inflorescence of *Liquidambar styraciflua* (Wisniewski & Bogle, 1982) supports this interpretation.

The primary or central axis of the total inflorescence elongates at anthesis, carrying the partial inflorescences ("heads") out of the bud and separating them through internodal elongation. The internodes may become progressively shorter toward the tip of the axis, and the most distal internodes may fail to elongate, resulting in the aggregation of a few distal heads into an irregular common mass. One or two functionally pistillate heads usually occupy the lowermost node(s) of the central axis, whereas the remaining nodes bear functionally staminate heads. However, completely pistillate or staminate total inflorescences are not uncommon.

The secondary axes, often referred to as the peduncles of the heads, originate in the axils of primary bracts of the primary axis, and show varying degrees of reduction. The proximal ones may elongate considerably, producing long- to short-stalked heads bearing secondary bracts with axillary flower clusters, whereas the more distal ones may fail to elongate at all, resulting in heads sessile on the primary axis. Failure of the distal internodes of the secondary axes to elongate results in terminal compound clusters of flowers similar to those at the tip of the primary axis.

The tertiary axes that bear the several flowers of each cluster are generally abortive, as are the floral pedicels (quaternary axes), resulting in the aggregation and fusion of the flowers.

An abscission layer forms in the primary axis just above the node bearing the uppermost pistillate head, allowing the entire staminate portion of the total inflorescence to fall after anthesis and pollination. The pistillate heads enlarge greatly in fruit and fall only after the seeds are shed in autumn. Artificial pollinations have shown the three principal species of *Liquidambar* to be interfertile (Santamour, 1972), but I know of no similar experiments in *Altingia*, or between *Altingia* and *Liquidambar*.

The individual flowers of *Liquidambar* and *Altingia* are morphologically bisexual, but typically are functionally unisexual. Stamens occur in the functionally pistillate flowers and range from typically abortive staminodia to rarely fertile. When fertile the viable pollen may be shed well after stigma receptivity in the same flower, preventing self pollination (Schmitt, 1965). Abortive carpel primordia or rudimentary ovaries occur in some staminate flowers, but ovules have not been observed. The inflorescences and flowers clearly are adapted to anemophily and outcrossing.

There are numerous conflicting observations in the literature regarding the presence or absence of a perianth in the Liquidambaroideae. Although there is general agreement that the staminate flowers of both genera lack a perianth, there are several reports of a perianth in the pistillate flowers of both *Liquidambar* and *Altingia*. I believe that these reports are based on misinterpretation of either: 1) the cycle of sterile stamens (as suggested by Horne, 1914); 2) the cycle of elongate sterile phyllomes (disc lobes) that occurs between the stamens and carpels in *Liquidambar formosana* and some species of *Altingia* (as *Semiliquidambar*); or 3) a layer of sclerenchymatous tissue that forms between and unites

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subulate phyllomes (pubescence of phyllomes and styles omitted.—F–H. Three variants of stamens with stylodeus connectives, bearing two or four sporangia. I–J. Diagrammatic representations of carpel vasculature in Liquidambaroideae.—I. Adjacent ventral bundles (v) free of any fusion.—J. Adjacent ventral bundles fused for a short distance basally (vv). Ovule traces shown for only one ventral bundle. (Key: d, dorsal carpel bundle; ov, ovule, ovule trace; st, stamen, stamen trace; stl, stylodeus stamen; sto, staminodium; tb, trunk bundle; v, ventral carpel bundle; vv, compound ventral bundle.)

the inferior portions of the flowers in the pistillate heads, and becomes protrusive as the heads dry out at maturity.

In *Liquidambar* various workers have described what they considered to be perianth parts (Oliver, 1867; Sargent, 1890, 1922; Ek, 1902; Sosa, 1978). Oliver (1867) apparently considered the sterile phyllomes of all three species of *Liquidambar* to be calycine. The indurated peripheral rim between flowers of mature heads of *L. styraciflua,* considered by Sargent (1890, 1922) to be a rudimentary calyx, is more probably formed by layers of bony tissue (possibly the "epidermal hairs" or "hair-like cells" of Schmitt, 1965) that externally delimit and unite the hypanthial walls of the fused, half-inferior ovaries that form the female partial inflorescences. The distal margins of these bony layers become protrusive in the surface of the head as the parenchymatous tissues of the fruits dry out and collapse.

Endress (1977) stated that "a perianth is almost totally lacking" in subfamily Liquidambaroideae, while Niedenzu (1891), Harms (1930), Samorodova-Bianki (1957), and Schmitt (1965) all found the pistillate flowers to lack a perianth in *Liquidambar.*

In *Altingia,* references to a perianth in the pistillate flowers are common. Blume (1828) apparently interpreted the sterile stamens as calyx lobes. Several workers described calyces united between flowers, but lacking a limb (e.g., Guillaumin, 1920; Hutchinson, 1967), or immersed in a disc with connate calyces fused with the stamens (Nakai, 1943). Several authors appear to have interpreted the sterile phyllomes (disc lobes) as part of the calyx limb (Griffith, 1836; Hooker & Thomson, 1858; Clarke, 1858; Niedenzu, 1891; Noronha, 1790), whereas the remainder believed that a perianth is almost totally lacking (Endress, 1977), or absent (Hemsley, 1906; Schulze-Menz, 1964; Tong, 1930; Wilson, 1905; Vink, 1957).

In *Semiliquidambar* H. T. Chang, Chang (1962) described the pistillate flowers as having confluent calyces with subulate calyx limbs ranging from 1–6 mm long. In a comparative chart he listed the calyx lobes as persistent or obscure in *Liquidambar,* persistent in *Semiliquidambar,* and lacking in *Altingia.* However, in fruits of *Altingia chingii* Metc. [= *Semiliquidambar chingii* (Metc.) Chang] that I have seen (*Lau 4356, Tso 20760,* both A) the only structures of the dimensions described are sterile phyllomes.

In the many specimens of *Liquidambar* and *Altingia* that I have examined I have found no evidence of calyx lobes or limb in any of the staminate or pistillate flowers at anthesis or beyond and have to conclude that none exist. Nor is there any evidence of a perianth in the earliest ontogenetic stages of *Liquidambar styraciflua* (Wisniewski & Bogle, 1982). However, I assume, as have others (Guillaumin, 1920; Hutchinson, 1967), that a calyx or calycine tissue was present in the ancestral line, forming a hypanthium that is now incorporated into the head as confluent tissue between the pistillate flowers. It may be this tissue that forms the interlocking "hair-like cells uniting the adjacent capsules" described by Schmitt (1965, fig. 2), and which eventually produces the sclerotic tissue uniting the ovaries of the flowers. I base my assumption that a perianth limb has been lost, rather than that the flowers were primitively naked, on comparative evidence from closely related subfamilies that also have their flowers fused in heads or spikes to some degree. In the dichlamydeous flowers of *Rhodoleia* (Rhodoleioideae) a very reduced, membranous, inconspicuous calyx is present. In the Exbucklandioideae (including Mytilarioideae H. T. Chang, 1973), *Mytilaria* is dichlamydeous with distinct calyx lobes, *Exbucklandia* is also dichlamydeous but shows evidence of a calyx only in the early stages of floral ontogeny, and *Chunia* lacks both calyx and corolla. *Disanthus* (Disanthoideae) is dichlamydeous, with distinct sepals and petals. It appears that reduction or loss of perianth in Liquidambaroideae, Rhodoleioideae, and Exbucklandioideae is related to condensation of inflorescences and increasing degrees of fusion between flowers in the heads. In this process, reduction and loss of the calyx limb may precede that of the corolla (Bogle, pers. observ.). Loss of the perianth has apparently occurred independently in both Liquidambaroideae and Exbucklandioideae, as well as in the more advanced members of the subfamily Hamamelidoideae (Bogle, 1970; Endress, 1970, 1978).

As is apparent from the foregoing discussion of the perianth, the interpretation of the cycle of sterile phyllomes (disc lobes) has been problematical. I have used the term phyllome (sensu Esau, 1965: 424, 540) to distinguish these organs from sterile and reduced stamens (staminodes), which commonly occur in pistillate flowers, because they show no direct relationship in structure or in transitional forms to stamens. Just as some authors considered them calycine, others have in-

terpreted them as bracteoles surrounding the pistillate flowers (Guillaumin, 1920); as vestigial styles of sterile flowers interspersed among the fertile flowers (Harms, 1930); as staminodia (Tong, 1930); as "disk" lobes (Vink, 1957); as papillae on the surfaces of the capsules (Schmitt, 1965); or as the sterile setae ("borsten") of *Liquidambar formosana* on which Harms (1930) based his section *Cathayambar*. Similar elongate sterile bodies, comparable to those seen in *L. formosana*, also occur in some species of *Altingia*, where I believe they have been interpreted as calyx lobes (H. T. Chang, 1962, 1973, as *Semiliquidambar*).

Croizat (1947) considered the lobes or sterile phyllomes to be "scales" arising "from the body of the head, or torus," and that the staminodia surrounding each flower "either belong to the scales that immediately surround the carpels, or to a row of subsidiary undeveloped scales abaxially located from these." He wrote that *Liquidambar* is "in active evolution away from the amentiferous stage, still retaining the head- or ament-like inflorescences and an ambiguous sexual expression, which leads on occasions to purely male or female heads or flowers."

However, the vascular supply to the phyllomes arises from the same trunk bundles as that of the stamens and carpels, and at a relatively high level within the flower. This does not support an interpretation of the phyllomes as extra-floral scales arising de novo from the torus. Neither does it support an interpretation of them as extra-floral organs of any kind.

Vink (1957: 364) emphasized the position of the sterile phyllomes (as "disk lobes") in *Altingia* and *Exbucklandia* (as *Symingtonia*) between the stamens and ovary. This position might suggest that they are staminodia, glandular tissue, or reduced sterile carpels.

Tong (1930: 9, 13, 14, fig. 2C, D) interpreted the phyllomes as staminodia, noted their spine-like ("stachelformig") form in *Liquidambar formosana*, and cited staminodia with functionless anthers as transition forms from stamens to staminodia in pistillate flowers of both *Liquidambar* and *Altingia*. His diagram (1930, fig. 2D) of the staminate flower of *Liquidambar* indicated two cycles of stamens. I have not observed this condition, nor have I seen any evidence of sterile phyllomes with abortive anthers. I have seen stamens with stylodeus elaborations of their connectives (Fig. 6E–H) external to the cycle of phyllomes, but the adjacent phyllomes show no such modification. The resolution of the proliferated vascular supply in the base of the phyllomes to a single, central vascular bundle in their distal portions could suggest the single bundle that normally supplies each stamen.

The short, blunt, glabrous phyllomes in *Liquidambar styraciflua* and some *Altingia* species look somewhat like similar organs in *Rhodoleia* and *Exbucklandia*, however. In *Rhodoleia* these organs form a cycle of very small, glabrous, irregular lobes inserted between the stamens and the ovary and are reported to be glandular (Leeuwen, 1938). In *Exbucklandia*, however, a cycle of blunt, glabrous, fleshy lobes is elevated on the inner rim of the hypanthium, and is clearly separated and distinct from the gynoecium. These lobes are not reported to function as glands, and their position on the rim of the hypanthium suggests a relationship to the androecium.

The proliferated system of procambial strands seen in the base of the sterile phyllomes or the stomata in the phyllome epidermis of *L. styraciflua* (Wisniewski & Bogle, 1982) might also suggest a glandular or secretory function, but there are no reports in the literature, nor any field observations of mine, that indicate such activity in these organs. Nor do the pubescent surfaces of the phyllomes of *Liquidambar formosana* and *Altingia chinensis* suggest a glandular function. In these species the epidermal trichomes of the phyllomes and the styles are similar and are not glandular.

A gynoecial origin could be inferred from the styliform phyllomes of *Liquidambar formosana*, and to a lesser extent from some specimens of *Altingia* (as *Semiliquidambar*) in which these organs approach the functional styles in length, and bear the same type of pubescence. Although they look very much like abortive carpels both at anthesis and in fruit, and have been interpreted as such (Harms, 1930), I have seen no evidence of stigmatic surfaces or ovule production in any of them. Many specimens of other species of *Liquidambar* and *Altingia* have relatively short, blunt, glabrous phyllomes, which sometimes appear to be inserted on the vestige of a hypanthial tube, apart from the ovary.

The late appearance of the phyllomes in ontogeny (Wisniewski & Bogle, 1982), after the stamens and functional carpels are initiated (at least in *Liquidambar styraciflua*) neither establishes nor eliminates a gynoecial relationship, but the ramifying vascular supply to the base of the phyl-

lomes does not appear comparable to that of the functional carpels.

A secondary origin of the sterile bodies might be hypothesized if some function relating to pollination or the reproductive process could be confirmed for them, as in *Rhodoleia*. On the other hand, the presence of similar whorls of sterile organs in such divergent genera as *Liquidambar, Altingia, Rhodoleia,* and *Exbucklandia* suggests an origin in a common ancestry, rather than a secondary origin related to reproductive processes.

It seems probable that the interpretation of the sterile phyllomes in Liquidambaroideae may relate directly to that of the similar organs in Rhodoleioideae, Exbucklandioideae, and Hamamelidoideae. If such fleshy, indeterminate organs were brought into close association with the developing gynoecium as a result of the condensation of the inflorescence, crowding of flowers, and eventual nearly complete fusion of hypanthium and gynoecium, morphogenetic factors might influence their development toward a stylodial morphology. That is not to suggest that Exbucklandioideae or Rhodoleioideae are in any way ancestral to the Liquidambaroideae, but rather that these groups probably shared a relatively close, common ancestral stock. The flowers of *Mytilaria* (Exbucklandioideae), with a dicyclic androecium in which the inner cycle of stamens appears to be sterile, and in which all stamens have remarkable fleshy, horned extensions of the anther connective, may provide clues as to the origin of the sterile phyllomes of the Liquidambaroideae. Additional ontogenetic studies in Liquidambaroideae, Rhodoleioideae, and Exbucklandioideae are needed.

The gynoecium in the Liquidambaroideae is the most primitive in the family. The carpels are follicular and unsealed. The shallow partial septum in the base of the unilocular ovary is characteristic of the family and becomes progressively more prominent in more advanced members of the family. The extensive stigmatic surfaces are clearly adapted for wind pollination. However, anemophily is probably a derived condition that has evolved several times within the family.

The carpel vascular supply of two marginal ventral bundles and a median dorsal bundle is comparable to that in the Rhodoleioideae, Exbucklandioideae, and Disanthoideae, and differs from the five bundle carpels of the Hamamelidoideae (Bogle, 1967, 1970). The ventral bundles of adjacent fused carpel margins may be distinct or fused basally for a short distance. The latter condition is shared with Rhodoleioideae and also becomes more pronounced in other subfamilies.

The large number of ovules per carpel, and their insertion in more than one row on both margins, is in keeping with the primitive condition of the carpels. Only the basal or sub-basal ovules on each margin are fertile, the remaining ovules are presumably sterile by reduction. The number of seeds produced per flower is very low in relation to the total number of ovules initiated in each flower. The tendency toward ovule abortion and reduction in number that characterizes the family, culminating in one ovule per carpel in some genera of Hamamelidoideae (Bogle, 1970), appears to be well established in the Liquidambaroideae.

Placentation has been described as either axile or parietal in the Hamamelidaceae. In the Liquidambaroideae the lowermost ovules may be inserted on the partial septum in the base of the ovary. This condition is sometimes termed axile placentation. Most of the ovules are inserted above the partial septum on the two lateral compound placentae, hence placentation is parietal. At a still higher level the uppermost ovules may be inserted on free carpel margins. Consequently, I use the term parietal as defined by Lawrence (1951: 763): "borne on the walls within a simple or compound ovary, or on intrusions of the wall that form incomplete partitions or false septa within the ovary."

There has been some disagreement concerning the taxonomic relationships of *Altingia* (Noronha, 1790) and *Liquidambar* (Linnaeus, 1753). They were considered to be congeneric under *Liquidambar* by several early workers (Blume, 1828; de Candolle, 1830; Lindley, 1836, 1853; Oken, 1841; Bentham, 1861), and more recently by Leroy (1982). Bentham and Hooker (1865) and other subsequent workers have recognized them as distinct genera.

The major differences between the two genera are the more or less elliptic to oblong, pinnately-veined, persistent leaves of *Altingia,* as opposed to the palmately-lobed and -veined, deciduous leaves of *Liquidambar*. The segregate genus *Semiliquidambar* H. T. Chang is described as being intermediate between *Altingia* and *Liquidambar* in this respect, with leaves polymorphous (trilobate, simple, or lobed on one side), triplinerved, and deciduous or not (H. T. Chang, 1962). *Semiliquidambar* occupies an extensive area of

overlap between *Altingia* and *Liquidambar formosana* in southeastern China and on the island of Hainan (distribution map in H. T. Chang, 1962). This distribution suggests that some of the specimens attributed to *Semiliquidambar* may have originated as hybrids between *Altingia* and *Liquidambar.* The appearance of the subulate phyllomes seen in the pistillate flowers of these specimens may thus be inherited from a *L. formosana* parent. Further morphological investigations of *Semiliquidambar,* and attempts at controlled hybridizations between *Altingia* and *Liquidambar* such as those conducted in *Liquidambar* by Santamour (1972), would be highly desirable.

A curious parallel can be seen between the Hamamelidaceae and Platanaceae in that similar contrasting leaf forms occur in *Platanus.* The tropical, southeast Asian *Platanus kerrii* has persistent, elliptic to oblong, penninerved leaves, whereas the remaining species of the genus have deciduous, palmately-lobed and -veined leaves. On the basis of these and other morphological characteristics, Leroy (1982) recently proposed the establishment of two subgenera in *Platanus* to separate these two divergent forms. Should the intermediate form attributed to *Semiliquidambar* eventually prove to originate in hybridization between *Altingia* and *Liquidambar,* these two genera might warrant similar taxonomic treatment.

Conclusions

It now seems clear that the total inflorescence in the Liquidambaroideae is more complex than was formerly thought. Four orders of axes (including the floral pedicels) are present, but only those of the first and second order are obvious. Primary and secondary inflorescence bracts are present, but tertiary bracts subtending individual flowers have not been observed.

The flowers are potentially bisexual, becoming functionally pistillate or staminate through failure of the stamens or carpels, respectively, to develop. Unisexuality is not completely established.

There is no morphological or anatomical evidence of a perianth in early ontogeny or in mature flowers. The perianth limb is assumed to have been lost phylogenetically as a function of inflorescence condensation leading to crowding and fusion of flowers. However, there is the suggestion of a brief hypanthial tube in the fused bases of the stamens and phyllomes.

The stamens are few and variable in number in each flower, dehiscing latrorsely by means of longitudinal slits. The connective often forms a fleshy cap above the sporangia in staminate flowers. Each stamen receives a single vascular trace.

The cycle of sterile phyllomes develops between the stamens and carpels of pistillate flowers. The phyllomes are not clearly staminodial or carpellary in form, origin, or vascularization and are not known to have glandular or secretory function or a role in pollination. They may relate directly to similar cycles of sterile organs in Rhodoleioideae and Exbucklandioideae.

The partly inferior ovary is usually bicarpellate. The carpels are involute and follicular, with numerous ovules on each margin, but usually have only one fertile ovule at the base of each margin. The carpel margins are not sealed in their apocarpous portions. Each carpel receives a dorsal and two ventral bundles. The ovules are supplied from the ventral bundles.

Although seemingly specialized and advanced within the family in such characteristics as inflorescence structure, tendency toward unisexual flowers, distinctive pollen morphology, and anemophily, the Liquidambaroideae, nevertheless, have a more primitive gynoecium (with follicular carpels, three distinct vascular bundles in each carpel, and numerous ovules on each margin) than any other genus in the family. The gynoecium of the Rhodoleioideae most closely approaches that of Liquidambaroideae, and that of the Disanthoideae shows considerable modification from both of those groups. The gynoecial structure, in particular, of Liquidambaroideae represents the least specialized condition in a family in which the general trend is toward reduction in the gynoecium, decrease in the number of ovules to one per carpel, and increased connation of carpels and carpel bundles. When this is taken in conjunction with such specialized characteristics as the presence of resin ducts, condensed inflorescences, unisexual flowers, rugate to porate pollen associated with anemophily, and sterile floral organs (phyllomes) of uncertain nature, each characteristic occurring in at least two other subfamilies, the Liquidambaroideae can be seen as part of a continuum or reticulum within the Hamamelidaceae, rather than as an independent family, the Altingiaceae.

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COMPARATIVE POLLEN MORPHOLOGY AND ITS RELATIONSHIP TO PHYLOGENY OF POLLEN IN THE HAMAMELIDAE[1]

MICHAEL S. ZAVADA[2,3] AND DAVID L. DILCHER[2]

ABSTRACT

Data on pollen morphological features from 200 species in 20 families commonly included in the Hamamelidae and particular species in the Anacardiaceae and Salicaceae are presented in this paper. The basic descriptive analyses presented are derived from observations by light microscopy, scanning electron microscopy (SEM), and transmission electron microscopy (TEM). Thirty pollen characters showed some variability, and each of the species was scored for these characters. These data were analyzed and similarity cluster analyses were generated. Both an unweighted pair group and a complete linkage strategy dendrogram were produced. Three major clusters of families were defined, based on these analyses. Group I consists of Trochodendraceae, Cercidiphyllaceae, Eupteleaceae, Platanaceae, Hamamelidaceae (including Altingioideae), Eucommiaceae, and Myrothamnaceae. The Liquidambaroideae, Eucommiaceae, and Myrothamnaceae, while closest to Group I, can be viewed as intermediate between Groups I and II in complete linkage strategy and between Groups II and III in unweighted pair group strategy. Group II—consisting of Daphniphyllaceae, Leitneriaceae, Barbeyaceae, and Fagaceae (excluding *Nothofagus*)—has a closer phenetic relationship to Group I than Group III. Group III is the largest of these groups: it consists of Ulmaceae, Cannabaceae, Juglandaceae, Rhoipteleaceae, Betulaceae, Casuarinaceae, and Myricaceae. The Balanopaceae and *Nothofagus* are somewhat isolated and peripheral entities but hold together in both linkage strategies. Thirty pollen characters of 78 taxa were analyzed using PAUP to produce a cladistic tree. The outgroup used was *Tetracentron*. Three phylogenetically related groups sorted out, which are the same as those already recognized in the Groups I, II, and III mentioned above. Group I occurs at the base of the tree (primitive), and Group II occurs as intermediate between Groups I and III (derived). In general, these data support the relationships suggested by Barabe for the Hamamelidae, based upon vegetative and floral features and the classification of Cronquist.

This survey of pollen in the Hamamelidae was initiated with three primary goals in mind: (1) to provide comparative morphological data for assessing the relationships of fossil-dispersed pollen with possible hamamelidaceous affinity, (2) to assess at which taxonomic level pollen characters of extant hamamelidaceous taxa are useful in determining taxonomic position, and (3) to assess the phylogenetic relationships of taxa within the Hamamelidae as elucidated by pollen morphology and ultrastructure.

To achieve these ends we used pollen data [transmission electron microscopy (TEM) and scanning electron microscopy (SEM)] from published literature and added pollen data from 42 previously uninvestigated taxa. We have amassed pollen data from 20 of the 24 families recognized by Cronquist (1981), representing over 200 species (Didymelaceae, Urticaceae, Moraceae, and Cecropiaceae are excluded from the cladistic and phenetic analyses). In addition, pollen data from the Anacardiaceae and Salicaceae are included in the analysis.

In a survey as broad as that presented here, it is often difficult to decide which taxa to include or exclude. Members of the Hamamelidae have been placed in a number of subclasses, and a comprehensive pollen survey of all the families of the different classifications was not attempted here. We decided to use the Cronquist (1981) system as a starting point and introduced into our analysis selected taxa from other subclasses that have been suggested to be phylogenetically related (e.g., Thorne, 1973).

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ANN. MISSOURI BOT. GARD. 73: 348–381. 1986.

Methods

All pollen was removed from dry herbarium material. A list of specimens used in this study and the herbarium data are presented in Appendix I. The pollen was first acetolyzed and prepared for TEM by dehydration in an ethanol series and embedded in Spurr's Low Viscosity Resin. Sectioning was done on an MT-2 ultramicrotome; the sections were post-stained in uranyl acetate and lead citrate for 15 minutes, respectively, and viewed on a Phillips EM-300. Acetolyzed pollen was prepared for SEM by mounting the pollen on stubs with the high vacuum wax Apiezon W-100 and coated with gold-palladium. A Cambridge Stereoscan scanning electron microscope was used for viewing.

The terminology used to describe aperture type, tectal and supratectal ornamentation, and pollen wall structure follows Faegri and Iversen (1964). Zavada (1984) discussed the criteria used to identify wall layers. Identification of wall layers relies not only on staining properties but also on some developmental data. However, very few developmental data on hamamelidaceous taxa are available; thus, pollen descriptions in this paper are based on the morphology and staining properties with the electron micrograph stains uranyl acetate and lead citrate.

Descriptive Palynology

TROCHODENDRALES

Trochodendraceae (1 genus, 1 species). This taxon is restricted to Japan and Formosa. Pollen of *Trochodendron aralioides* Sieb. & Zucc. is tricolpate, oblate to slightly prolate. Pollen is about 24 μm in polar diameter and 20 μm in equatorial diameter (Erdtman, 1952). Exine sculpturing is reticulate. Wall structure is tectate-columellate with a relatively thick footlayer. A thin endexine is evident (Praglowski, 1974; Walker, 1976).

Tetracentraceae (1 genus, 1 species). This species is found in China and Burma. Pollen of *Tetracentron sinense* Oliv. ex Hook. is tricolpate, spherical to slightly prolate. Pollen averages about 15 μm in diameter. Exine sculpturing is reticulate (Walker, 1976). Pollen wall structure is tectate-columellate with a footlayer that is underlain by an endexine, which thickens slightly in the apertural region (Praglowski, 1974).

CERCIDIPHYLLALES

Cercidiphyllaceae (1 genus, 1–2 species). Cercidiphyllum japonicum Sieb. & Zucc. is endemic to Japan. Pollen is tricolpate (Walker, 1976; this study) or pericolpate (Walker, 1976; Fig. 1). Pollen averages 36 μm in polar diameter and 31 μm in equatorial diameter (Erdtman, 1952). Pollen shape is spherical to prolate. Exine sculpturing is reticulate (Fig. 1). Pollen wall structure is tectate-columellate with a footlayer of varying thickness (Fig. 2). A thin endexine that does not thicken in the apertural region is evident (Praglowski, 1974; Fig. 2).

EUPTELEALES

Eupteleaceae (1 genus, 2 species). Euptelea pleiosperma Hook. f. & Th. is found in China and India, and *E. polyandra* Sieb. & Zucc. is endemic to Japan. Pollen of *E. polyandra* was studied and is predominately tricolpate (Walker, 1976; this study); however, pericolpate grains have been reported (Praglowski, 1974; Walker, 1976). Shape varies from oblate to prolate (Fig. 3). Pollen ranges between 29 and 39 μm in polar diameter (Erdtman, 1952). The exine sculpturing is reticulate (Fig. 3). Pollen wall structure is tectate-columellate with a thin footlayer (Fig. 4). Endexine underlies the footlayer and is thin in nonapertural regions but thickens somewhat in apertural regions (Praglowski, 1974; this study).

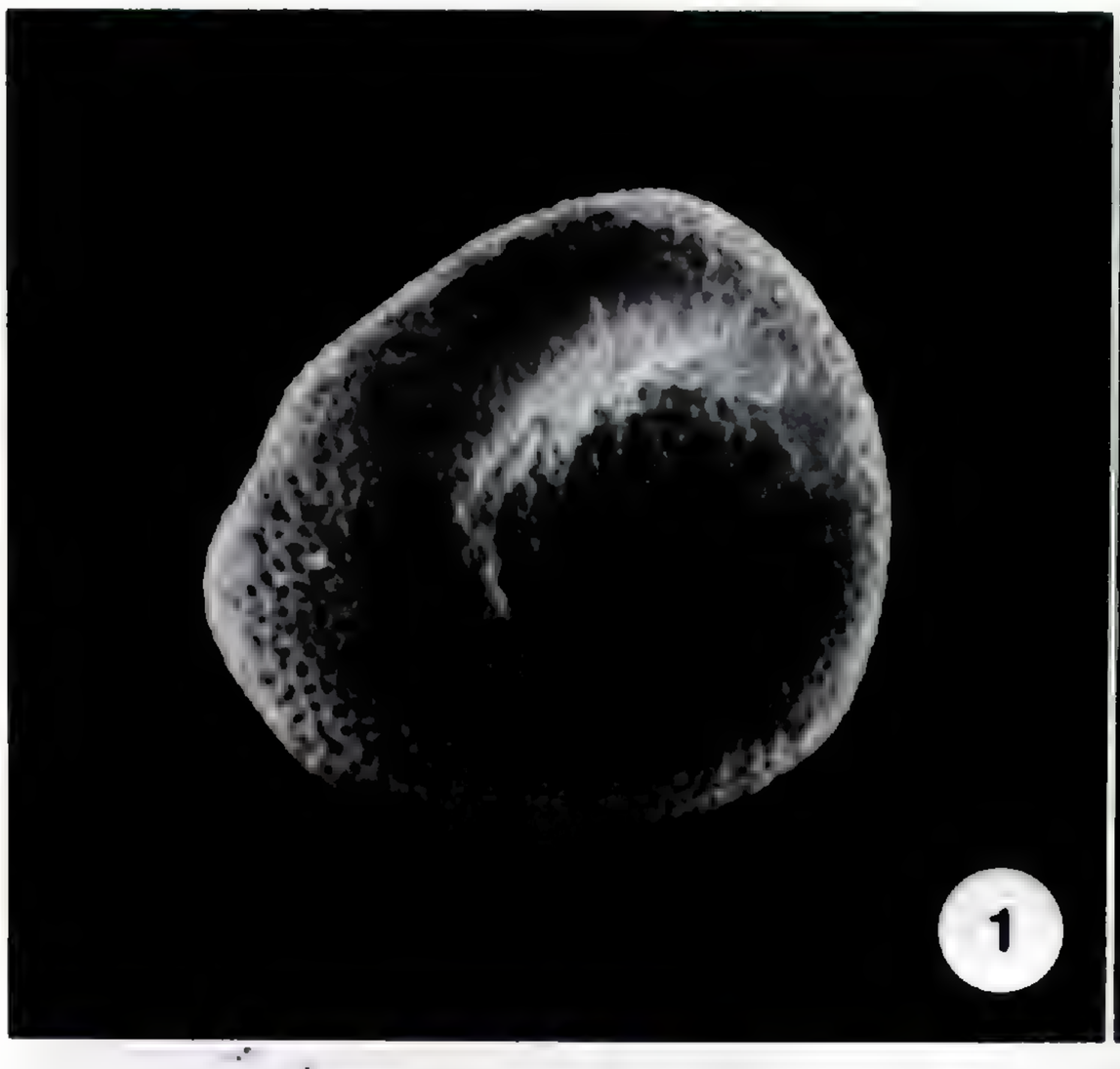
HAMAMELIDALES

Platanaceae (1 genus, 7–12 species). Platanus is widely distributed in temperate and subtropical regions of the Northern Hemisphere. Pollen of seven species was studied with SEM and TEM (Appendix I) and one species was studied by Hesse (1978) using TEM. Pacltova (1982) presented a methodological study of the pollen of some recent and fossil species of *Platanus*.

Platanaceae are a stenopalynous family. All species studied are treated together due to their morphological and ultrastructural similarity.

Pollen is tricolpate (Figs. 5, 6, 8, 11), the colpi are lenticular (Fig. 5) to slightly ovoid (Fig. 11). The grains are spherical to slightly prolate in equatorial view and circular to semi-angular in polar view and 19–24 μm in polar diameter and 17–22 μm in equatorial diameter. The exine sculpturing is reticulate (Figs. 5, 6, 8, 9, 11), the wall structure is tectate-columellate with a footlayer the same thickness as the tectum (Figs. 7, 10, 12–14). A thin endexine may be present (Figs. 7, 10, 13, 14); however, this may be an artifact of staining in some taxa (Fig. 12).

Myrothamnaceae (1 genus, 2 species). This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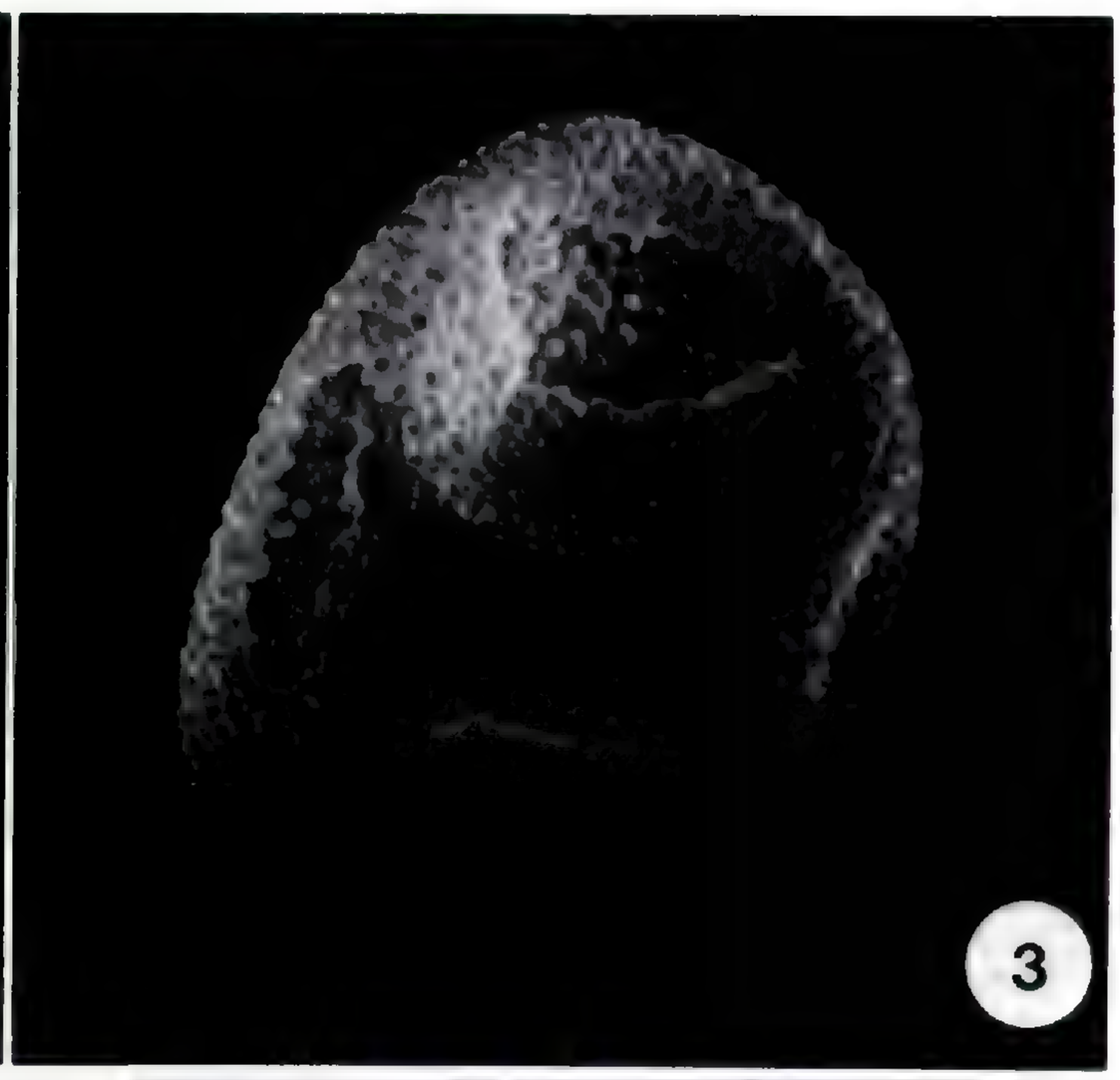
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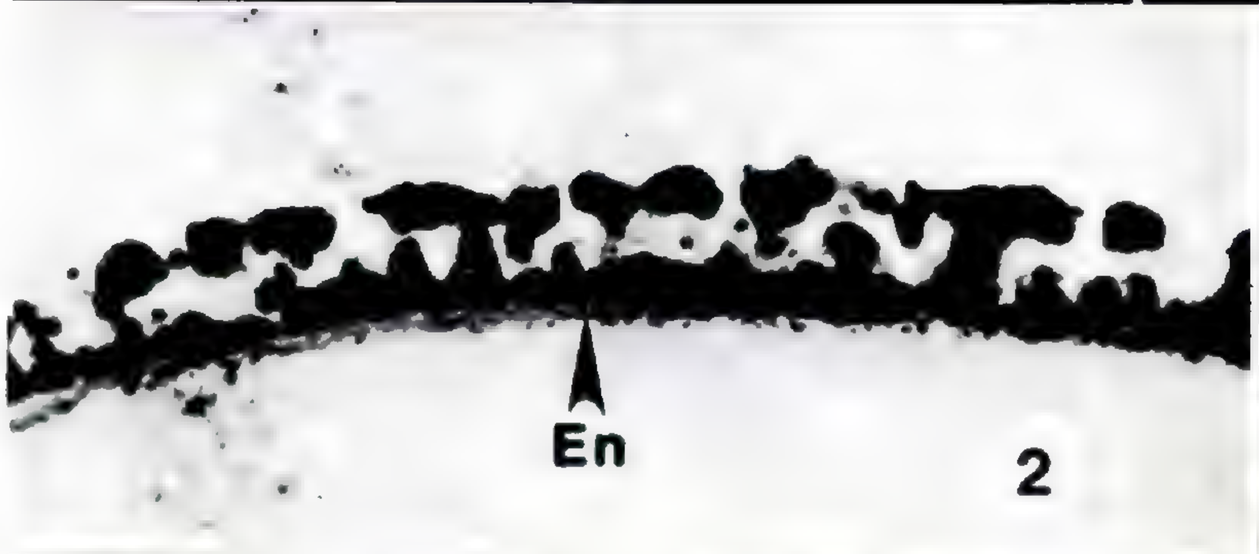

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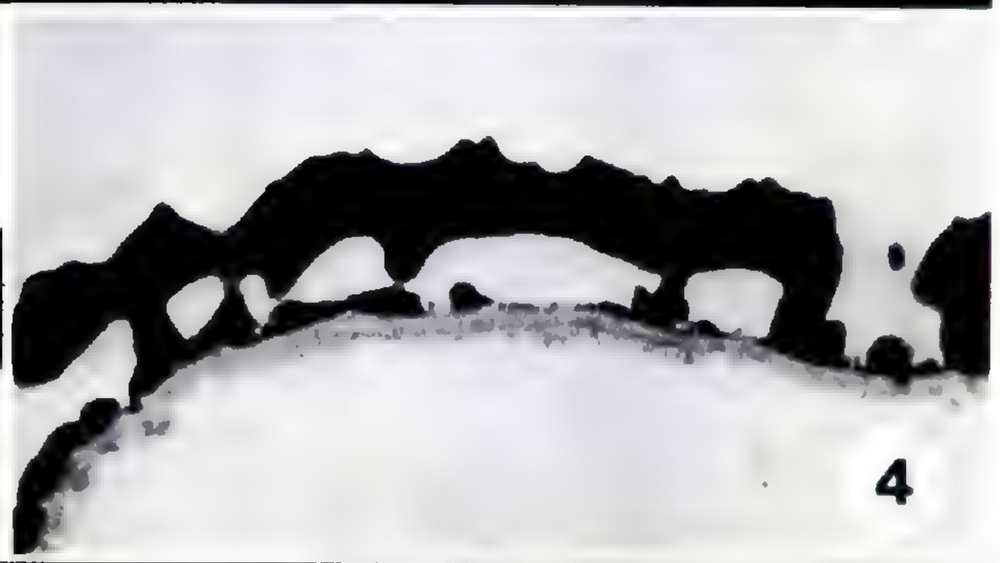
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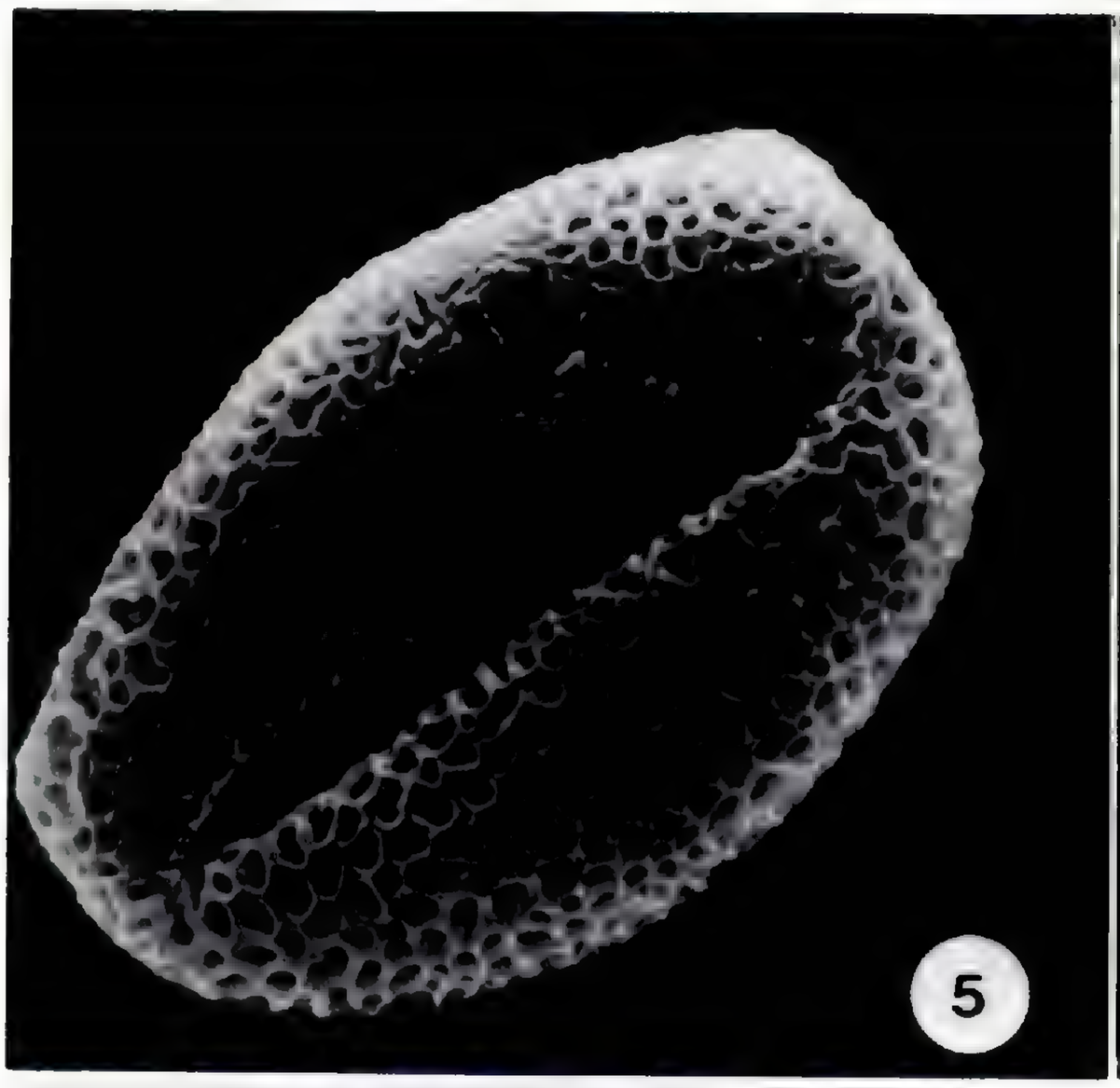
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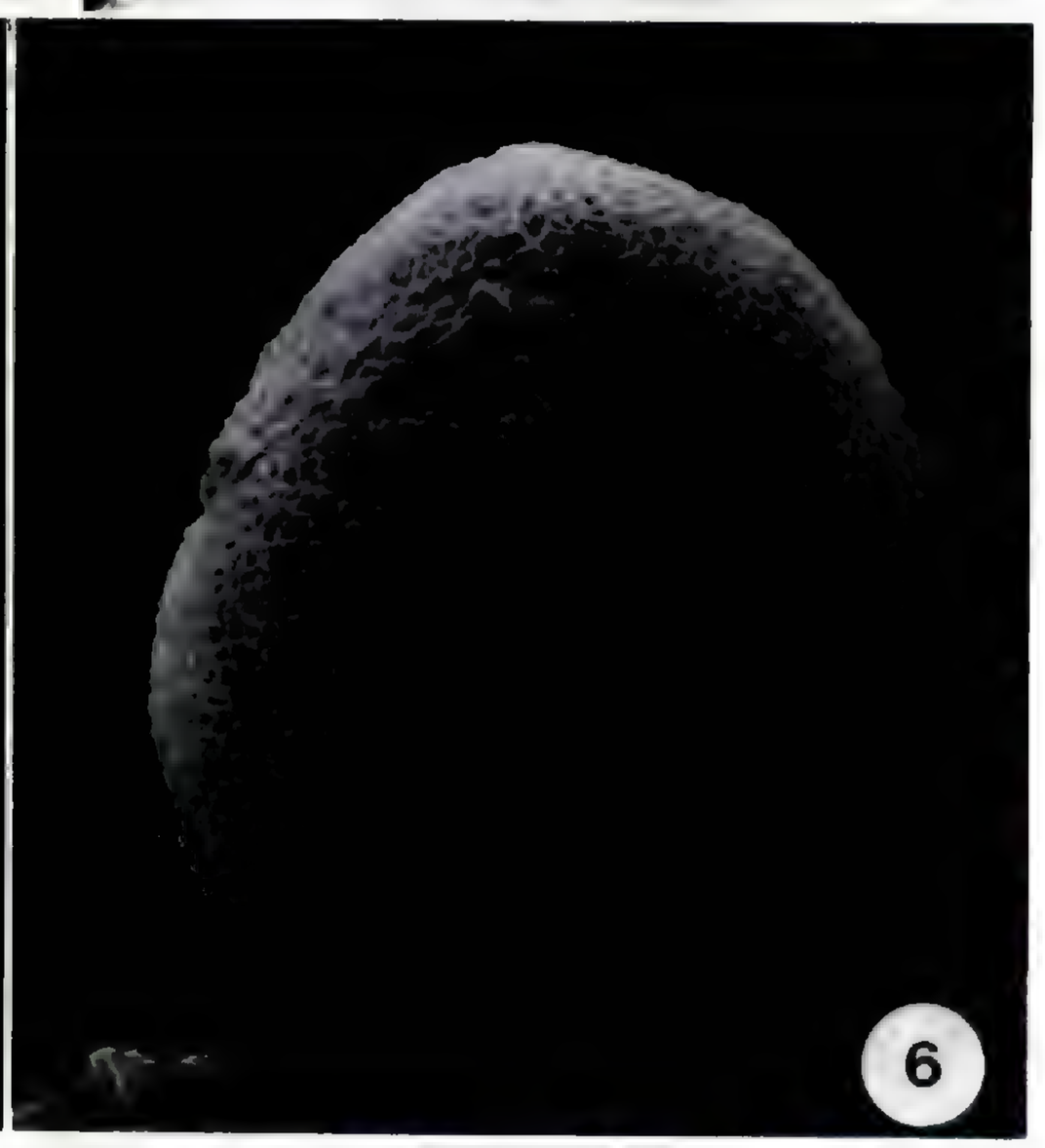
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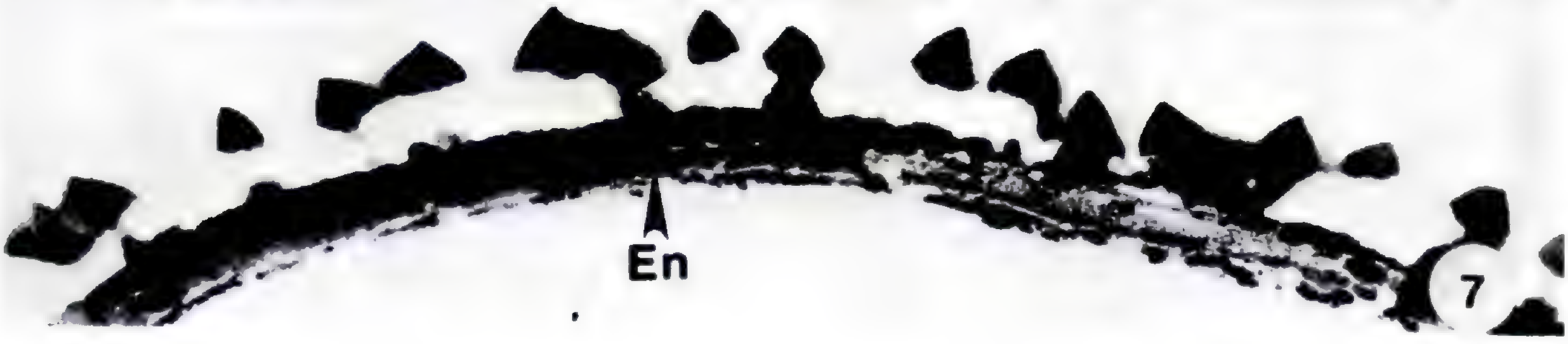

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family of xerophytic shrubs consists of *Myrothamnus moschatus* Baill. in Madagascar and *M. flabellifolia* Welw. in South Africa.

The pollen of *Myrothamnus moschatus* Bail. and *M. flabellifolia* Welw. is usually shed in tetrahedral tetrads (occasionally in tetragonal tetrads) that range between 23 and 25 μm in diameter for *M. moschatus* and 24 and 26 μm for *M. flabellifolia* (Figs. 15, 19, 21). Single pollen grains of *M. moschatus* range between 11 and 14 μm in polar diameter and 12 and 15 μm in equatorial diameter. The pollen of *M. flabellifolia* ranges between 12 and 15 μm in polar diameter and 13 and 16 μm in equatorial diameter. Pollen in both taxa is spherical and triporate (Fig. 21). The three somewhat circular, ill-defined pores are symmetrically positioned and distally offset from the equator. The exine sculpturing consists of clavate processes that are ornamented with minute papillae (Figs. 16, 18, 20, 22). The wall averages 0.7 μm in thickness and is intectate. The pollen wall structure consists of an outer columellate layer. The columellae are the clavate processes easily observed with SEM (Figs. 16–20) and the bases of the clavate columellae are fused to a footlayer (Figs. 18–20) that is at times discontinuous (Fig. 18). Beneath the footlayer is a thin endexine that is not thickened adjacent to the apertural region (Fig. 18). In the region where pollen grains are joined in the tetrad, the columellae are short, stout pegs, and their apices are joined and hold adjacent pollen together (Figs. 17, 19).

The only interspecific differences are that the clavate processes in *Myrothamnus moschatus* are more widely spaced than in *M. flabellifolia* (compare Figs. 16 and 22). In addition, the footlayer in *M. moschatus* is usually thicker than the footlayer of *M. flabellifolia*. However, due to the lack of fertile herbarium material, intraspecific variation is unknown and we do not know how consistent these differences are within wide-ranging populations.

Hamamelidaceae (28 genera, 100 species). This family has a cosmopolitan distribution. Pollen of 12 genera (out of 28) and 16 species (out of 100) was studied ultrastructurally. Bogle and Philbrick (1980) examined 28 genera using SEM. Hesse (1978) described the ultrastructural characteristics of three genera and four species, and Endress (1977) illustrated eight taxa using SEM. The taxa investigated are treated here on the subfamilial level.

Liquidambaroideae. Pollen of *Liquidambar styraciflua* L. and *Altingia obovata* Merr. & Chun were studied with TEM and SEM. Bogle and Philbrick (1980) examined *L. orientalis* Mill. and *A. chinensis* Oliv. ex Hance using SEM. The pollen is spherical, periporate, the pores circular, often with islands of ektexine on the pore membrane (Fig. 31), and 32–58 μm in diameter. Exine sculpturing is finely reticulate with small supratectal rugulae, the wall structure is tectate-columellate, with a footlayer that is the same thickness as the tectum (Figs. 31, 32). The columellae are thin and short in *Liquidambar* (Fig. 31) but somewhat thicker in *Altingia* (Fig. 32). The footlayer is often underlain by a thin, less electron-dense wall layer (presumably endexine) that does not considerably thicken in the apertural region (Figs. 31, 32).

Rhodoleiodeae. Pollen of this monotypic subfamily (*Rhodoleia championii* Hook. f.) was studied with TEM (this study) and SEM (Bogle & Philbrick, 1980). Pollen is tricolpate, shape is subprolate, and 16–26 μm in equatorial diameter and 20–29 μm in polar diameter (Bogle & Philbrick, 1980). Exine sculpturing is finely reticulate (= scrobiculae of Bogle & Philbrick, 1980), and the wall structure is tectate-columellate with a footlayer as thick as the tectum (Fig. 29). The endexine appears as a thickened layer in the apertural region only (Fig. 29).

Exbucklandioideae. Pollen of *Exbucklandia populnea* (R. Br. ex Griff.) R. W. Brown was studied with SEM (Bogle & Philbrick, 1980; this

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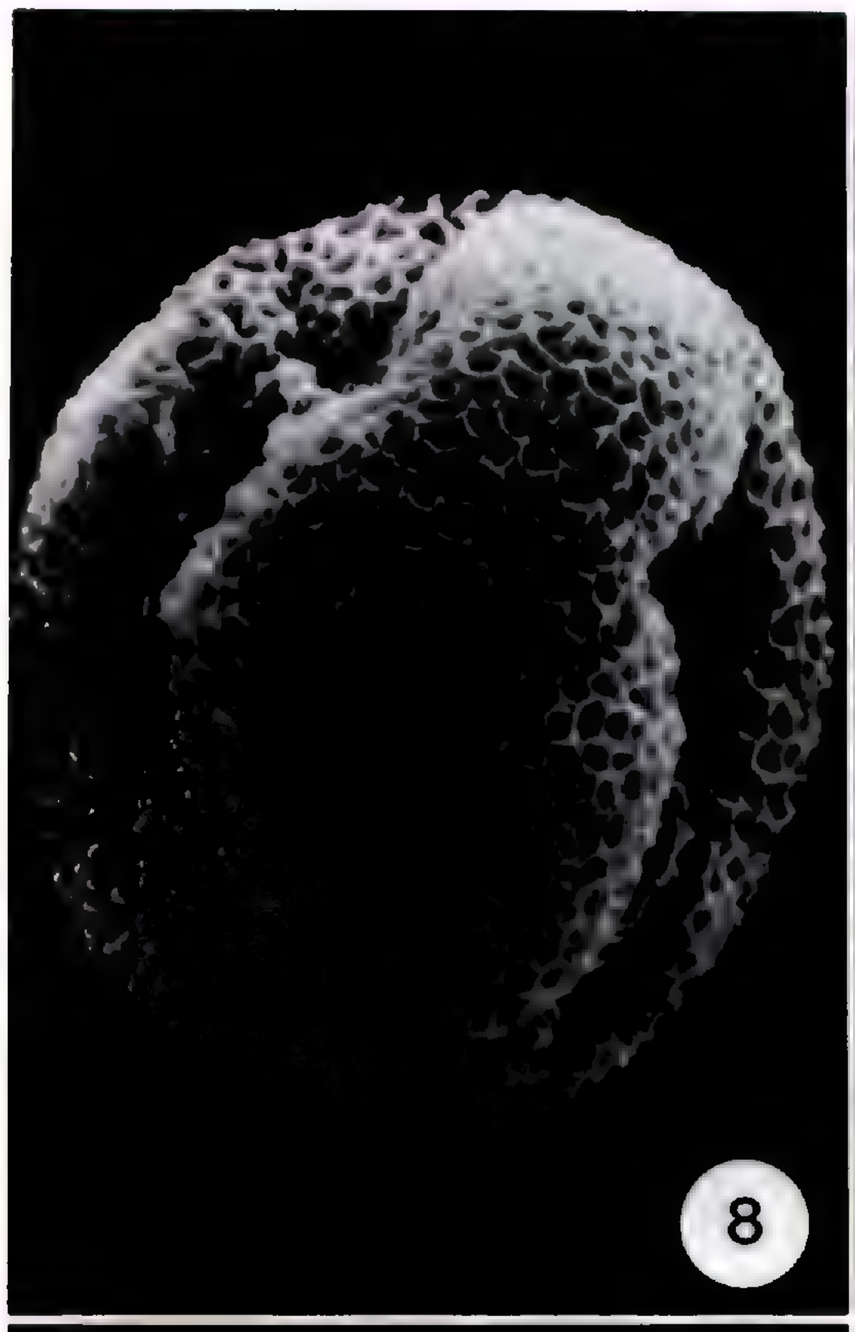
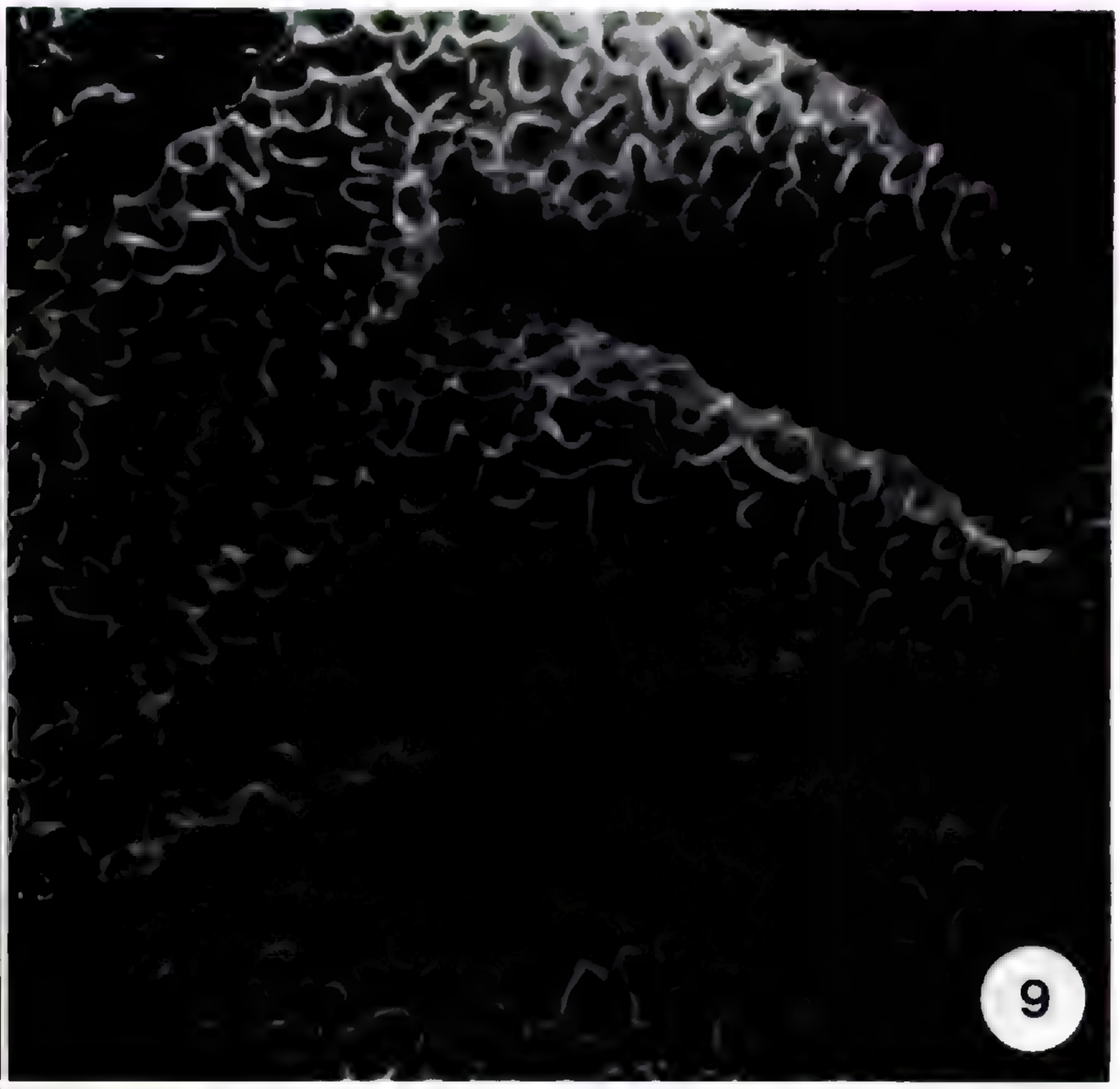
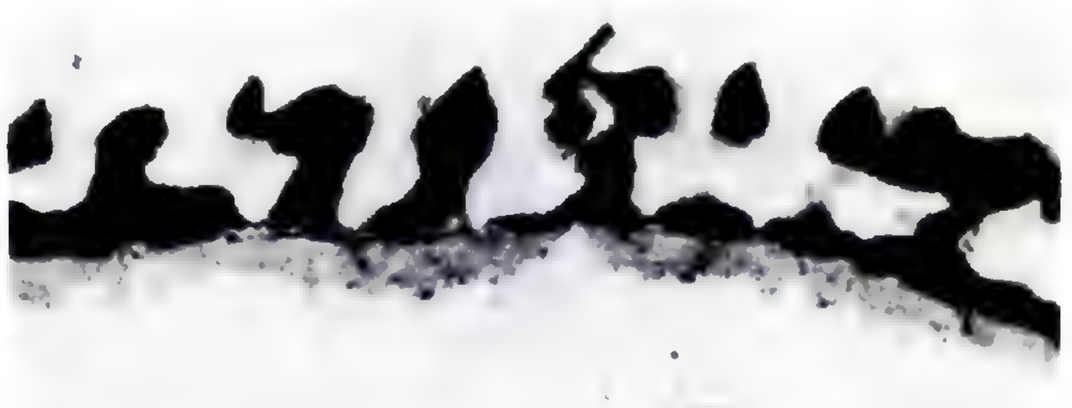
FIGURES 1–7.—1. Scanning electron micrograph of *Cercidiphyllum japonicum* showing reticulate exine sculpturing; × 1,300.—2. Transmission electron micrograph of *C. japonicum* showing tectate-columellate wall structure, footlayer, and thin endexine (En); ×14,660.—3. Scanning electron micrograph of *Euptelea polyandra* showing reticulate exine sculpturing and pericolpate apertures; ×1,300.—4. Transmission electron micrograph of *E. polyandra* showing tectate-columellate wall structure, thin footlayer, and less dense endexine; ×14,600.—5. Scanning electron micrograph of *Platanus acerifolia*; ×3,100.—6. Scanning electron micrograph of *P. mexicana*; ×3,200.—7. Transmission electron micrograph of *P. acerifolia* showing tectate-columellate wall structure, footlayer, and possible endexine (En); ×16,200.







FIGURES 8–14.—8. Scanning electron micrograph of *Platanus occidentalis*; ×3,200.—9. Scanning electron micrograph of *P. occidentalis* showing aberrant apertures, not an uncommon occurrence in this taxon; ×5,800.—10. Transmission electron micrograph of *P. occidentalis* showing tectate-columellate wall structure, footlayer, and possible endexine; ×12,600.—11. Scanning electron micrograph of *P. kerrii*; ×3,100.—12. Transmission electron micrograph of *P. kerrii* showing identical wall structure to the other *Platanus* species; however, differential staining of endexine is not very evident; ×12,540.—13. Transmission electron micrograph of *P. rzedowski*; ×10,260.—14. Transmission electron micrograph of *P. racemosa* showing identical wall structure to other *Platanus* species; ×16,200.

study) and TEM (this study). Pollen of *Mytilaria laosensis* Lecomte and *Chunia bucklandioides* H. T. Chang was studied with SEM by Bogle and Philbrick (1980).

Pollen is tricolpate and spherical to prolate in all three taxa and 26–32 μm in equatorial diameter and 23–37 μm in polar diameter in *E. populnea*, and 26–37 μm in equatorial diameter and 29–38 μm in polar diameter in *C. bucklandioides*. Exine sculpturing is reticulate in *Exbucklandia populnea* and *Mytilaria laosensis* and finely reticulate in *Chunia bucklandioides*. Pollen wall structure of *E. populnea* is tectate columellate with a thin footlayer (Fig. 23). No endexine is evident.

Disanthoideae. Pollen of *Disanthus cercidifolius* Maxim. is tricolpate, spherical to prolate, ranging between 22 and 23 μm in equatorial diameter and 22 and 33 μm in polar diameter, exine sculpturing is reticulate. Wall structure is tectate-columellate with a thin footlayer (Fig. 26). The endexine is thin in nonapertural regions but thickens in the apertural region.

Hamamelidoideae. This is the largest subfamily, with 21 genera. All genera were studied with SEM (Bogle & Philbrick, 1980) and six genera were investigated with TEM [*Hamamelis* (3 spp.), *Lorapetalum* (1 spp.), *Corylopsis* (2 spp.), *Fothergilla* (2 spp.), *Matudaea* (1 spp.), this study; and *Parrotia* (1 sp.), Hesse, 1978].

In most taxa, pollen is tricolpate but varies from tricolpate to pericolpate in *Fothergilla*, and is periporate in *Sycopsis*, tetracolpate to periporate in *Distylium*, and pericolpate in *Matudaea*. Pollen varies from slightly oblate to mostly spherical and prolate and is 16–53 μm in diameter. Exine sculpturing is finely reticulate to coarsely reticulate, often with supratectal verrucae. In all taxa studied with TEM, pollen wall structure is tectate-columellate with well-developed footlayers (Figs. 25, 27, 28, 30). Endexine is evident in *Fothergilla monticola* Ashe (Fig. 28), *Corylopsis pauciflora* Sieb. et Zucc. (Fig. 27), and *Matudaea hirsuta* Lundell (Fig. 30), but absent in *Parrotia persica* (DC.) C. A. Mey. (Hesse, 1978), *Hamamelis japonica* Sieb. et Zucc. (Fig. 24), and *Lorapetalum chinense* Oliv. (Fig. 25).

DAPHNIPHYLLALES

Daphniphyllaceae (1 genus, 35 species). This monotypic order is distributed in eastern Asia and the Malay Archipelago. Five species were investigated with SEM and TEM (Appendix I). Pollen is tricolpate (Figs. 33, 35, 39, 41), spherical to oblate in equatorial view (Figs. 33, 39) and circular in polar view (Figs. 35, 37), 17 μm in polar diameter and 21 μm in equatorial diameter (Erdtman, 1952). Exine sculpturing is somewhat psilate to verrucate (Figs. 34, 36, 38, 40, 42), the wall structure is tectate-columellate with a thin footlayer, and the tectum is occasionally perforated with small channels (Figs. 36, 40, 41). Endexine is present and is thin in nonapertural regions (Figs. 36, 40) but thickens considerably in the apertural region (Figs. 34, 38, 42).

DIDYMELALES

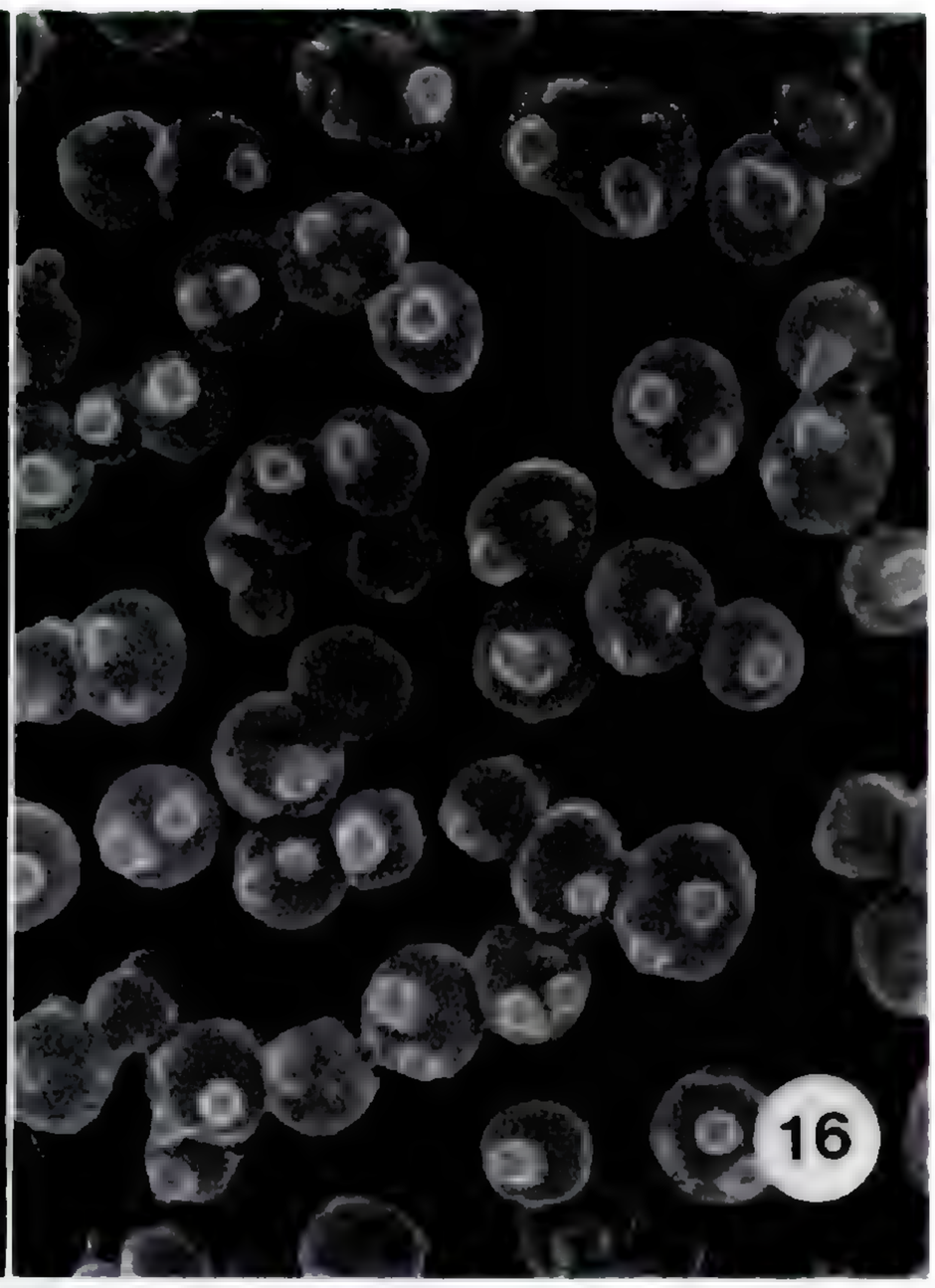
Didymelaceae (1 genus, 2 species). This family is restricted to Madagascar. Pollen is tricolpate with two pores per colpus: one in the distal hemisphere and one in the proximal hemisphere, oblate to spheroidal, about 21 μm in equatorial diameter and 23 μm in polar diameter, exine sculpturing is reticulate (Erdtman, 1952). Little is known of pollen wall structure but it appears to be tectate-columellate with a footlayer. Occurrence of endexine is unknown (Erdtman, 1952).

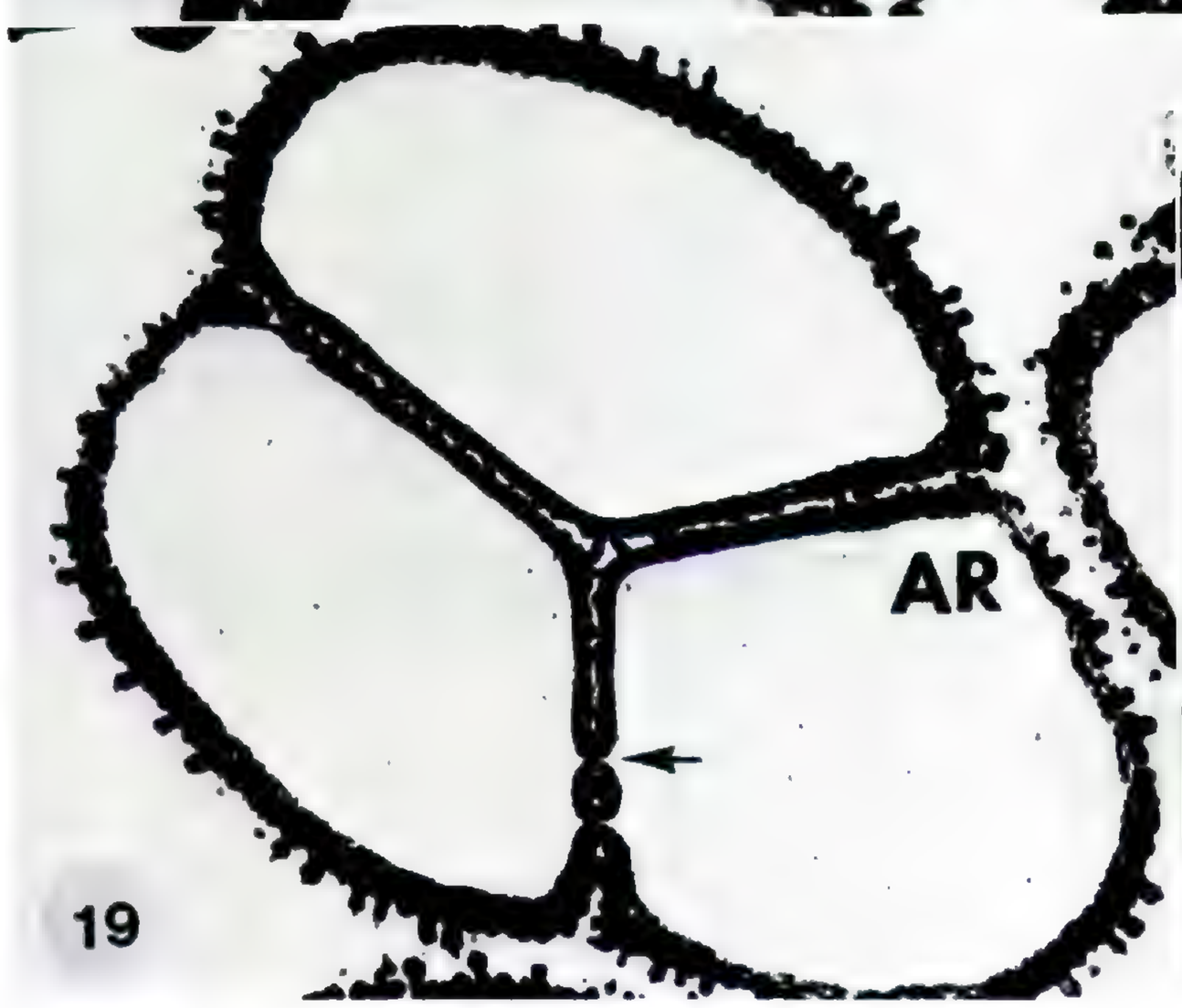
EUCOMMIALES

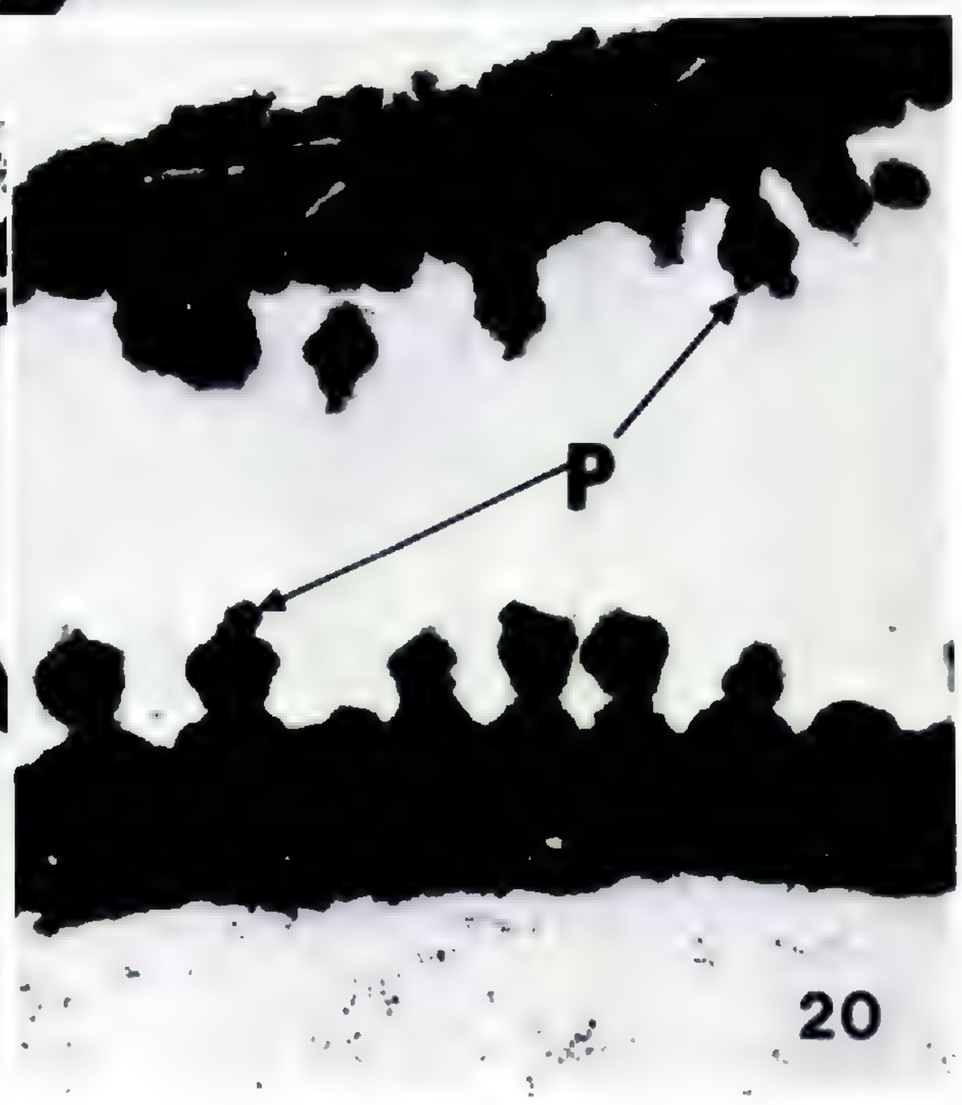
Eucommiaceae (1 genus, 1 species). Eucommia ulmoides Oliv. is found in China. Pollen is prolate and tricolpate: one colpus narrows near the equator but expands in the polar region (Fig. 43), the two other colpi appear straight (Fig. 44). The pollen is about 42 μm in polar diameter and 31 μm in equatorial diameter (Erdtman, 1952). Exine sculpturing is minutely spinulose to verrucate (Figs. 43, 44). Pollen wall structure is atectate, the ektexine homogeneous (Figs. 45–47), a rather thick endexine is present that does not thicken in the apertural regions (Figs. 45–47).

LEITNERIALES

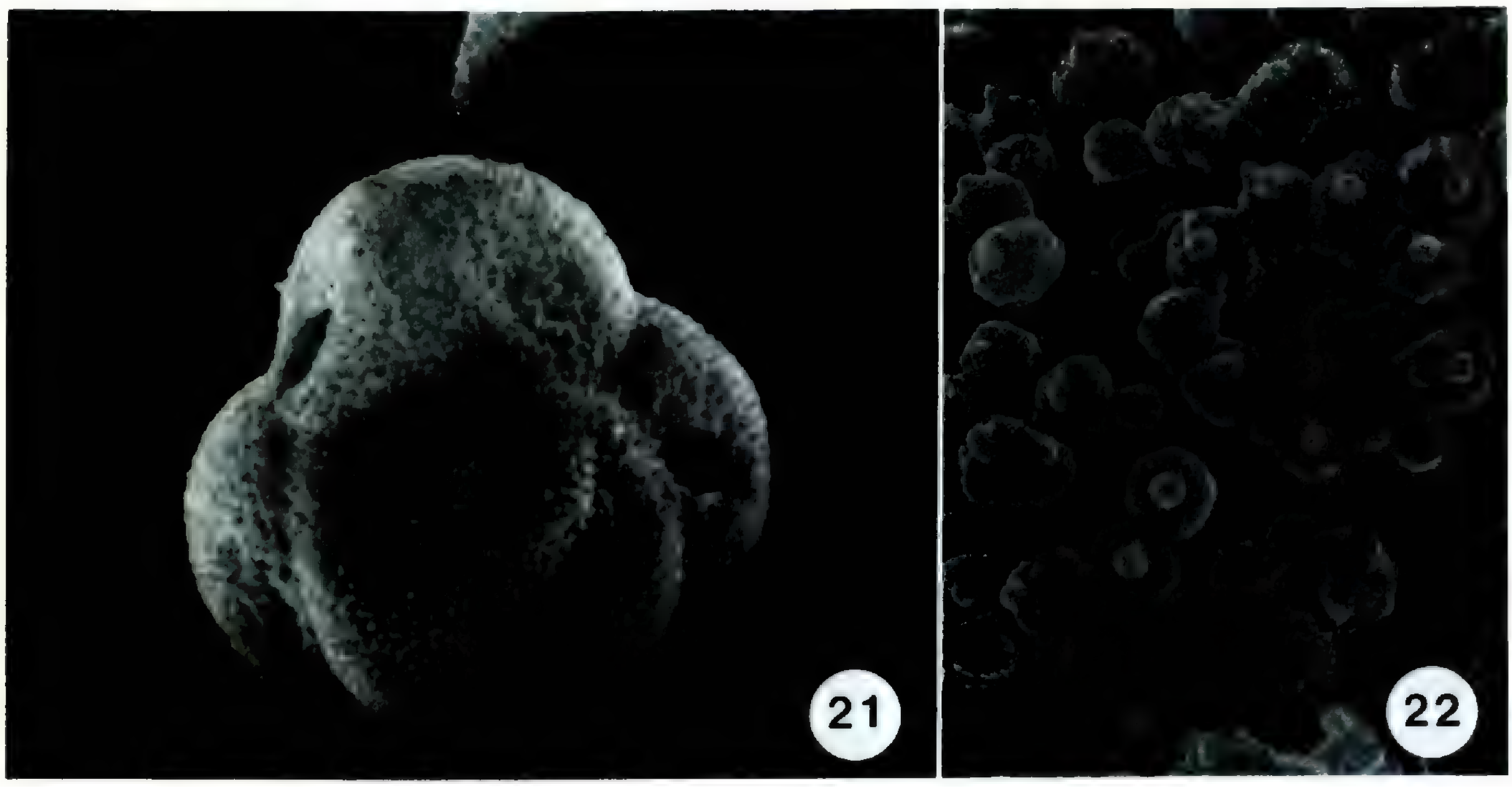
Leitneriaceae (1 genus, 1 species). This monotypic family occurs in the southeastern United States (*Leitneria floridana* Chapm.). Pollen was studied with SEM and TEM. Pollen is tricolporate (occasionally tetracolporate), oblate to spheroidal (Fig. 48), 26–28 μm in size (Erdtman, 1952). Exine sculpturing is minutely verrucate (Fig. 49); the tectum is microperforate (Fig. 50), the wall structure is tectate-columellate with







FIGURES 15–20.—15. Scanning electron micrograph of *Myrothamnus moschatus* showing tetrahedral tetrad with clavate exine sculpturing; ×1,300.—16. Scanning electron micrograph of *M. moschatus* showing clavae with minute papillae; ×15,500.—17. Transmission electron micrograph of *M. flabellifolia* showing attachment of pollen in a tetrad. Note thin endexine (arrow); ×8,094.—18. Transmission electron micrograph of *M. flabellifolia* through the distal face of a pollen grain adjacent to the apertural region (AR). Note thin endexine (arrow), which does not thicken near the aperture and discontinuous footlayer (e.g., above arrow); ×6,840.—19. Transmission electron micrograph of *M. moschatus* showing attachment of pollen in a tetrad. Note inter-



FIGURES 21, 22.—21. Scanning electron micrograph of *M. flabellifolia* showing a tetrahedral pollen tetrad, clavate sculpturing, and porate aperture (A); ×2,000.—22. Scanning electron micrograph showing clavae with minute papillae. Note that the clavae are more crowded than in *M. moschatus* (compare with Fig. 16); ×15,500.

a very thin footlayer (Fig. 50). An endexine is present in nonapertural areas and thickens considerably in apertural regions.

URTICALES

Barbeyaceae (1 genus, 1 species). *Barbeya oleoides* Schweinfurth occurs in northeast Africa. Pollen was studied with SEM and TEM. Pollen is tricolporate (pores are equatorially elongate and wider than the colpi), oblate to spheroidal (Fig. 52), about 26 μm in polar diameter and 22 μm in equatorial diameter (Dickison & Sweitzer, 1970; this study). Exine sculpturing is scabrate (Figs. 52, 53). Pollen wall structure is tectate-columellate with a thick tectum traversed by microperforations (Fig. 51), the tectum is underlain by short, stout columellae (Fig. 51). The columellae rest on what appears to be endexine (Fig. 51). The footlayer is essentially absent. The endexine thickens somewhat in apertural regions.

Ulmaceae (15–17 genera, 150–200 species). The family is distributed throughout temperate and tropical regions of the world and is usually divided into two subfamilies, Ulmoideae and Celtidoideae. Some pollen has been studied with SEM and TEM (Zavada, 1983).

Ulmoideae. The pollen is 4–7-stephanoporate, the pores circular to elliptical, spheroidal to angular in polar view and oblate to spheroidal in equatorial view (Fig. 54), 31 μm in diameter. The exine is generally rugulate, the rugulae correspond to thick areas of the pollen wall (Fig. 54; except in *Planera,* which is psilate). Pollen wall structure consists of a tectum occasionally traversed by minute channels, granular infrastructure, and a thin continuous footlayer (Fig. 55). No endexine is evident (Zavada, 1983).

Celtidoideae. The pollen is 2–5-stephanoporate, the pores circular to slightly elliptical, circular to semi-angular in polar view and oblate to spheroidal in equatorial view, about 20 μm in diameter. Exine sculpturing is scabrate to finely verrucate (Fig. 56), and wall structure consists of an outer tectum that has minute channels. The infrastructure consists of a middle layer of anastomosing rods and an inner layer of irregular-shaped columellae, which rest on a thin basal layer (Fig. 57; Zavada, 1983).

Cannabaceae (2 genera, 2 species). This family occurs in north temperate regions. Pollen of *Cannabis sativa* L. was studied with SEM and TEM. Pollen is triporate with annulate pores; the

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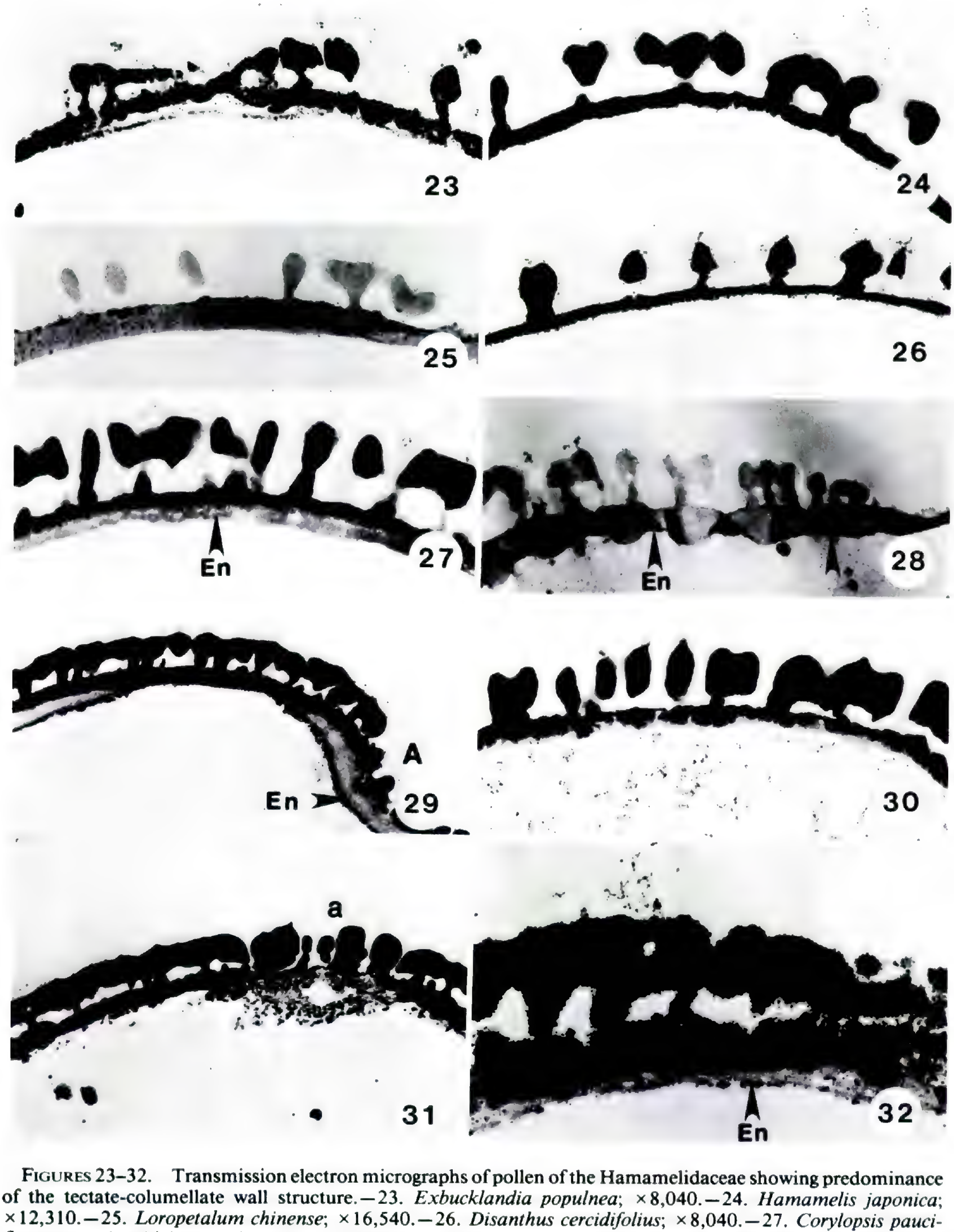
cytoplasmic channels (arrow) and the thin endexinal apertural membrane (AR); ×3,876.—20. Transmission electron micrograph of *M. moschatus* of the distal face of a pollen grain showing clavae with minute papillae (P) and thick basal layer. In this particular section, endexine does not stain differently than ektexine; ×15,960.



FIGURES 23–32. Transmission electron micrographs of pollen of the Hamamelidaceae showing predominance of the tectate-columellate wall structure.—23. *Exbucklandia populnea*; ×8,040.—24. *Hamamelis japonica*; ×12,310.—25. *Loropetalum chinense*; ×16,540.—26. *Disanthus cercidifolius*; ×8,040.—27. *Corylopsis pauciflora*, note the thick endexine (En); ×16,540.—28. *Fothergilla monticola*, note dark-staining discontinuous endexine (En, arrows); ×12,310.—29. *Rhodoleia championii*, note endexine (En) adjacent to apertural region (A); ×16,540.—30. *Matudaea hirsuta*; ×16,540.—31. *Liquidambar styraciflua* (A = apertural area); ×5,600.—32. *Altingia obovata*, note thin endexine (En); ×12,310.

annulus around the pore is formed by an elaboration of the infrastructural layer in this region (Text-Fig. 7F), (Fig. 58), oblate, 30 μm in equatorial diameter. Exine sculpturing is finely spinulose (Hamilton, 1976; this study), and wall structure is tectate-granular (often interspersed among the granules are thin columellae-like structures) with a thin footlayer (Fig. 59) and what appears to be a very thin endexine.

Moraceae (including the Cecropiaceae) (40 genera, 1,000 species). This family is widespread in subtropical and tropical regions of the world. For the size and importance of this family, little is known palynologically. However, a few taxa have been studied ultrastructurally (Niezgoda & Nowaczyk, 1976; Hamilton, 1976; Punt, 1978; Punt & Eetgerink, 1981). Pollen is variable and, in the taxa studied, it is di-stephano- or periporate, spherical to oblate, and averages about 30 μm in diameter. Exine sculpturing can be rugulate to scabrate with small supratectal spinules. Pollen wall structure (only studied in *Dorstenia* sp.; this study) is tectate-granular with a bilayered basal layer (Fig. 73). The tectum is occasionally traversed by minute channels.

Urticaceae (45 genera, 700 species). This family is widely distributed in subtropical and tropical regions of the world. Pollen wall ultrastructure is unknown. Pollen is stephano- or periporate, predominantly oblate, and 10–20 μm in diameter (Erdtman, 1952). Exine sculpturing is scabrate to rugulate with supratectal spinules (Hamilton, 1976).

JUGLANDALES

Rhoipteleaceae (1 genus, 1 species). Rhoiptelea chiliantha Diels et Hand is native to southeast Asia. Pollen has been studied with SEM and TEM by Stone and Broome (1971). The pollen is oblate, tricolporate with very short colpi appearing to approximate the triporate condition, averaging 27 μm in equatorial diameter. Exine sculpturing is scabrate, pollen wall structure is tectate-granular, and the infrastructural area is underlain by a footlayer. The tectum is traversed by minute channels. A thin endexine is evident.

Juglandaceae (8 genera, 60 species). This family is widely distributed in temperate and tropical regions of the Northern Hemisphere. The pollen was studied with SEM and TEM by Stone and Broome (1975). They recognized the four basic pollen types described below.

Engelhardtia-type—Pollen is triporate (varies from 2 to 8), oblate, 14–26 μm in diameter, and lacks pseudocolpi.

Platycarya-type—Pollen is triporate (varies from 2 to 5), oblate, 15–16 μm in equatorial diameter with pseudocolpi.

Carya-type—Pollen is triporate (varies from 1 to 6), oblate, and 33–66 μm in diameter.

Pterocarya-type—Pollen is stephanoporate, oblate to spheroidal, and 28–50 μm in equatorial diameter.

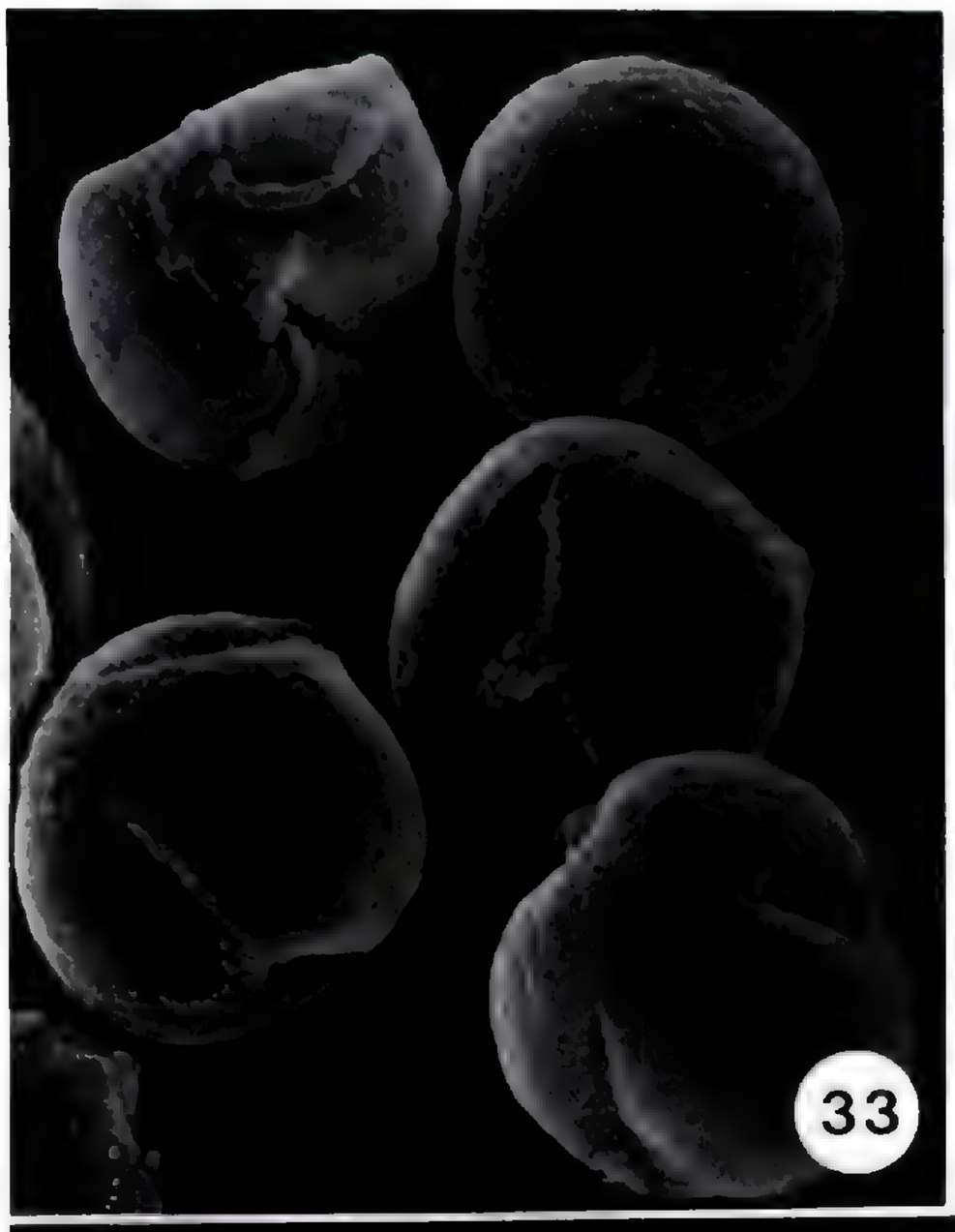
Pollen wall structure in all of the above taxa is tectate-granular with a relatively thick footlayer. The tectum is occasionally traversed by minute channels. A thin endexine is often present that does not thicken in the apertural region (Stone & Broome, 1975).

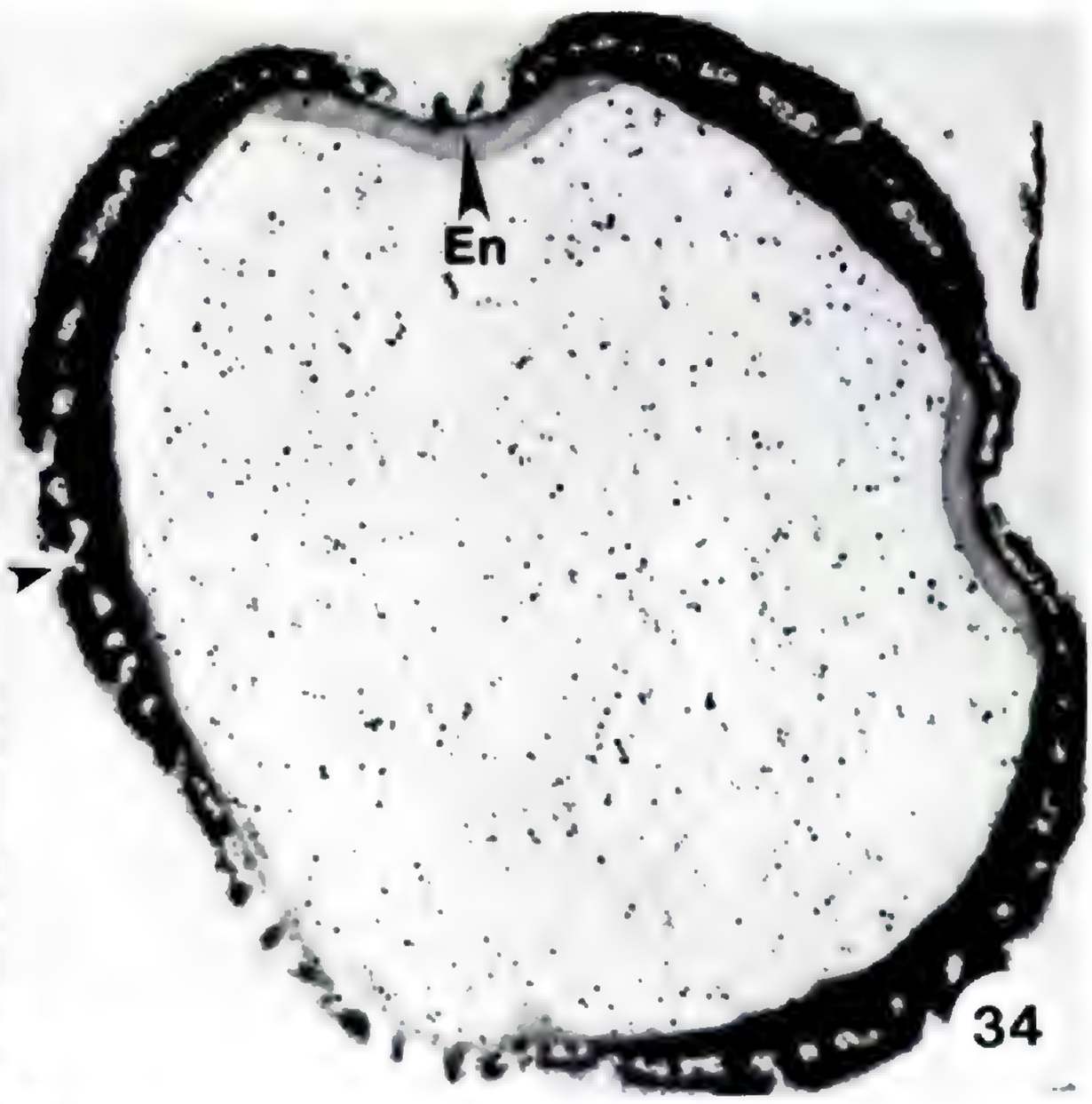
MYRICALES

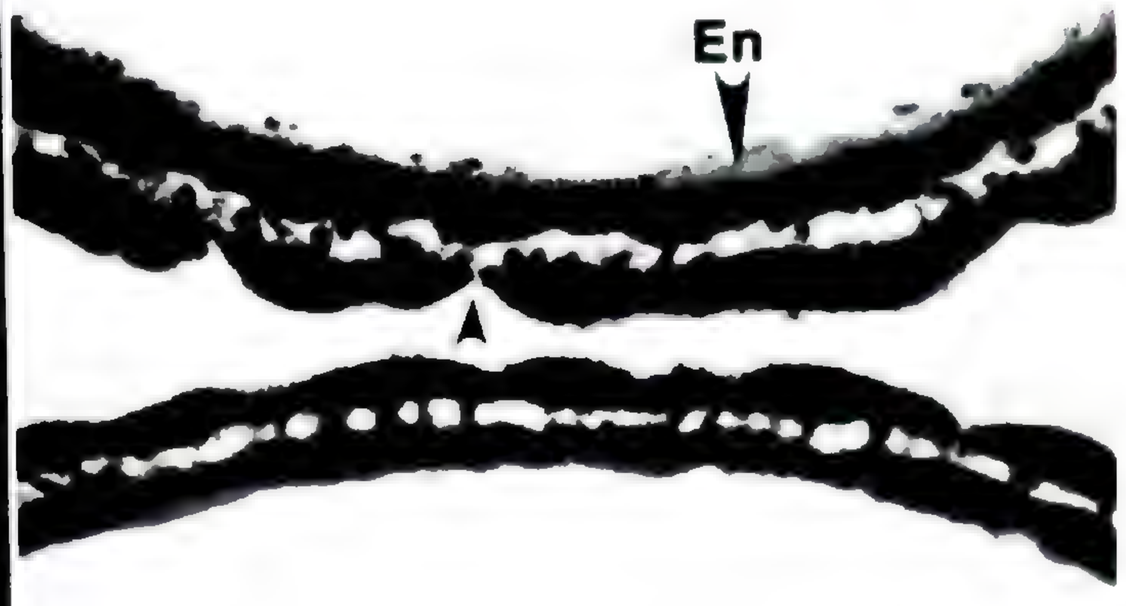
Myricaceae (3 genera, 50 species). This family is distributed in temperate and subtropical regions. Pollen is triporate, oblate, about 26 μm in equatorial diameter. Exine sculpturing consists of small scabrae (Praglowski, 1962; Lieux, 1980). Pollen wall structure of *Myrica asplenifolia* L. was studied with TEM (Fig. 64), and Coetzee and Praglowski (1984) investigated 11 species of *Myrica* with SEM and TEM and found that the pollen in those species is 21–25 μm in polar diameter, 25–35 μm in equatorial diameter. The pollen wall structure is tectate-granular; however, stout columellae are often discernable in the infrastructural layer (Fig. 65). The tectum is traversed by minute channels (Fig. 65). A relatively thin footlayer is present; no endexine is evident.

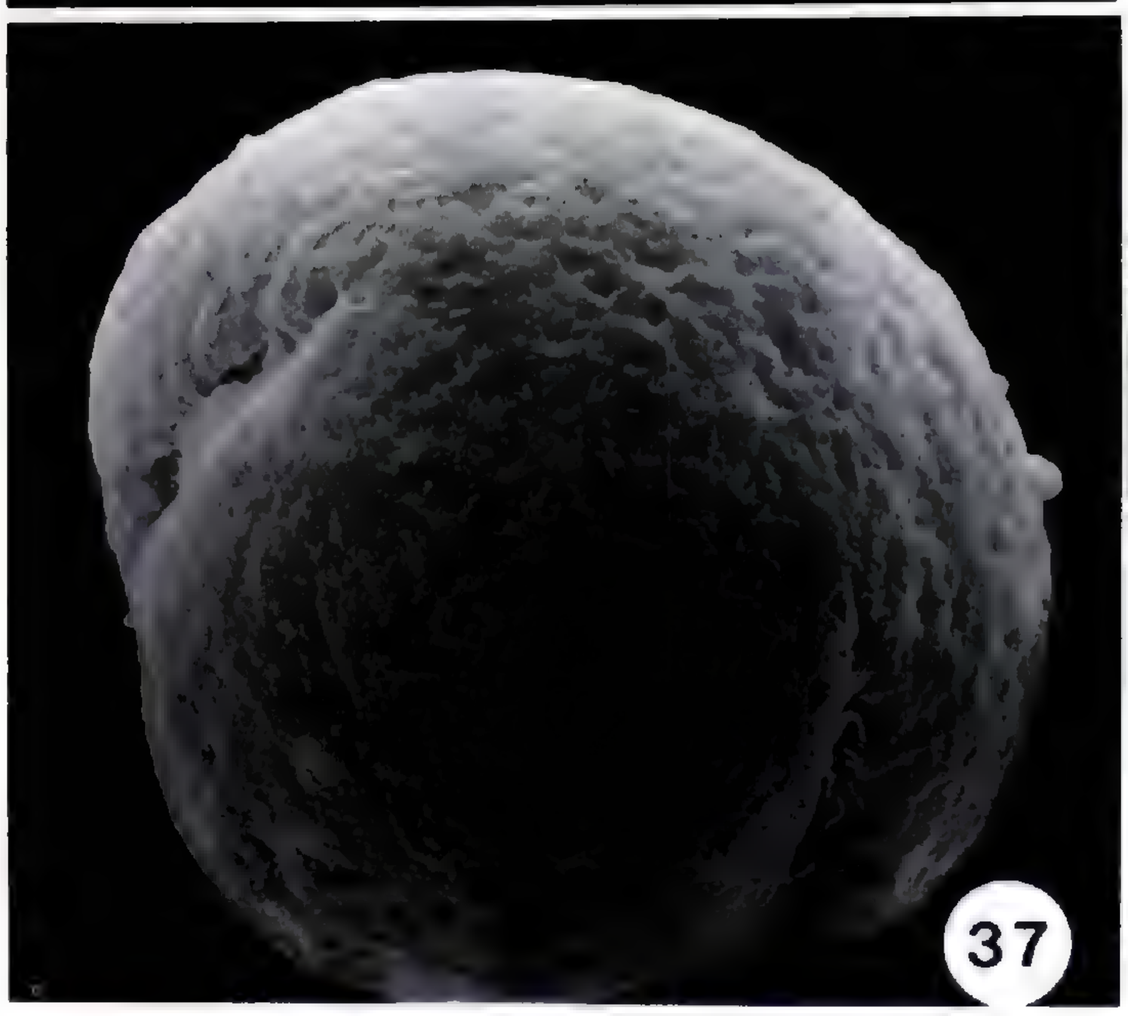
FAGALES

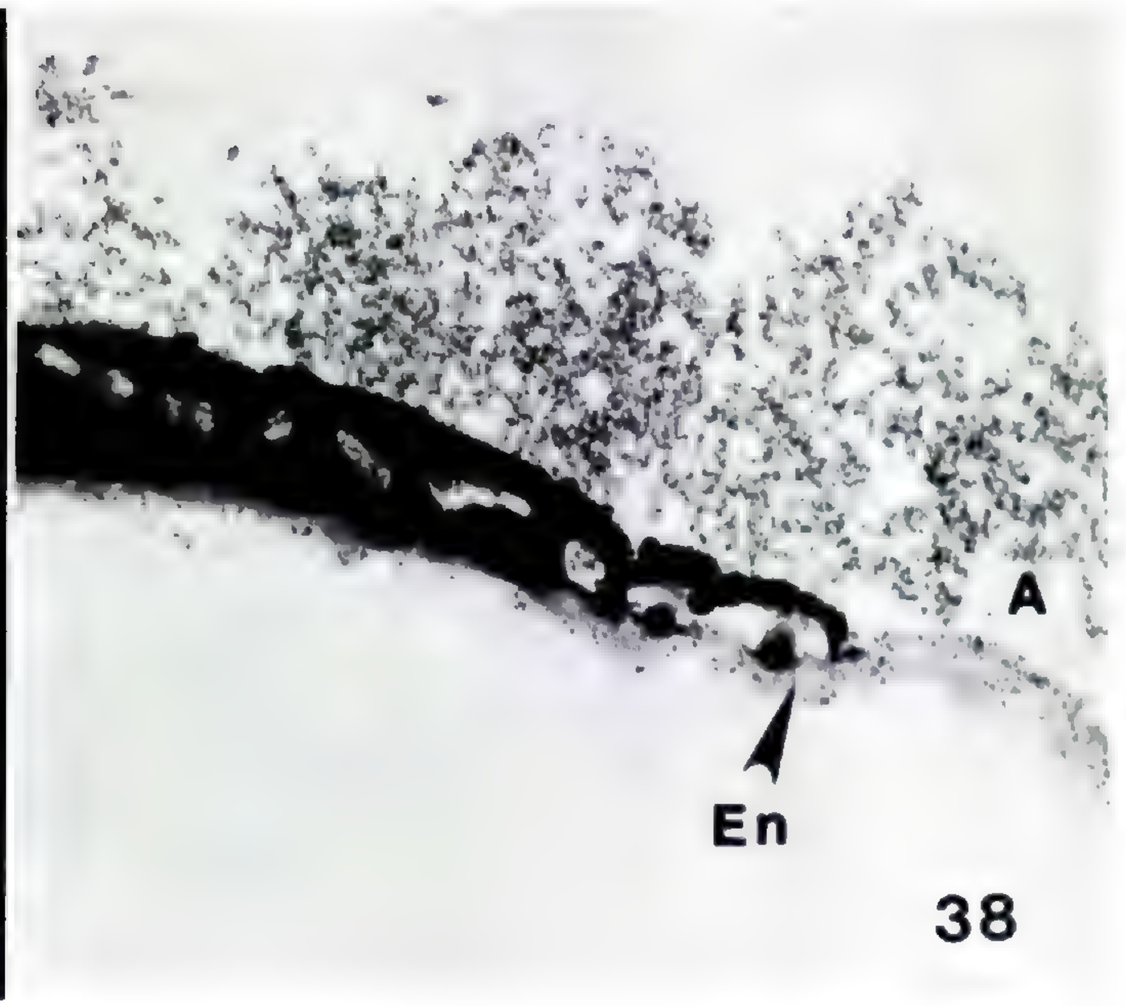
Balanopaceae (1 genus, 9 species). This family is distributed in regions of the southwest Pacific (e.g., New Caledonia). Pollen of *Balanops vitiense* (A. C. Smith) Hjedruqvist is 3–5-colpate, oblate, averaging 35 μm in diameter (Erdtman, 1952). The exine sculpturing consists of small spinules (Fig. 68), the wall structure is tectate-granular to columellate (Fig. 69), and the tectum is traversed by microperforations. The infrastructure consists of both irregular-shaped granules and robust columellae that rest on an uneven and sometimes discontinuous footlayer (Fig. 69). The footlayer is underlain by an endexine that,



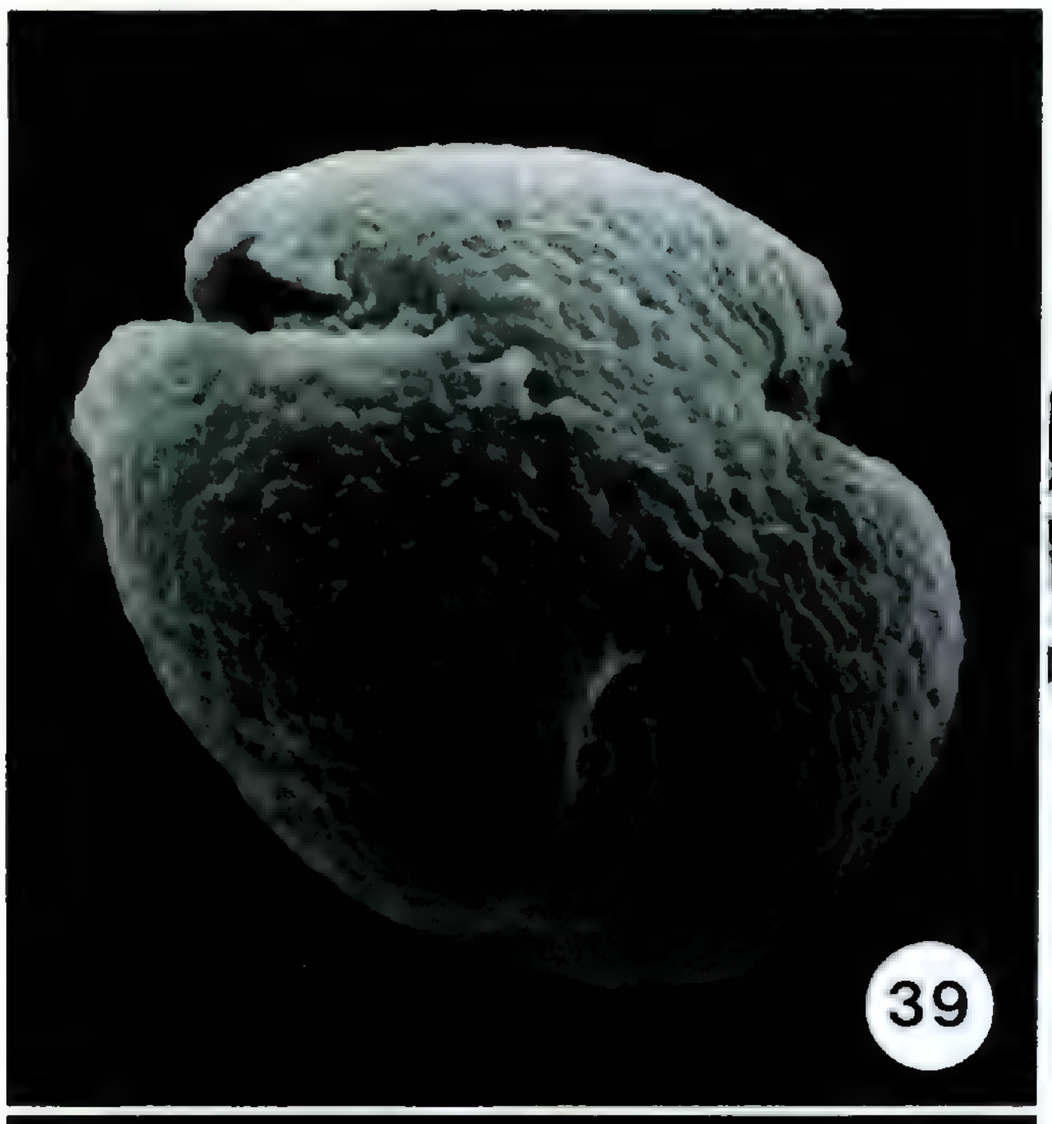


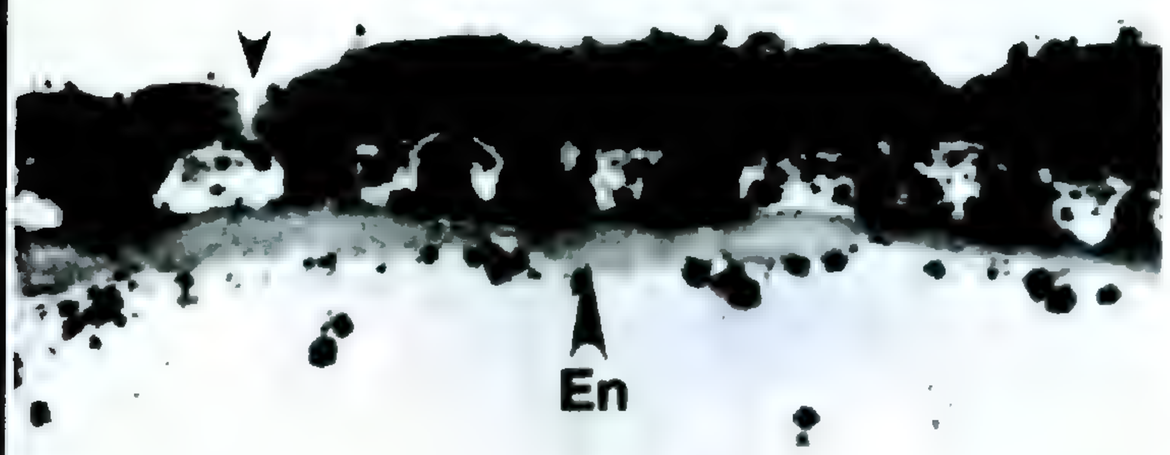


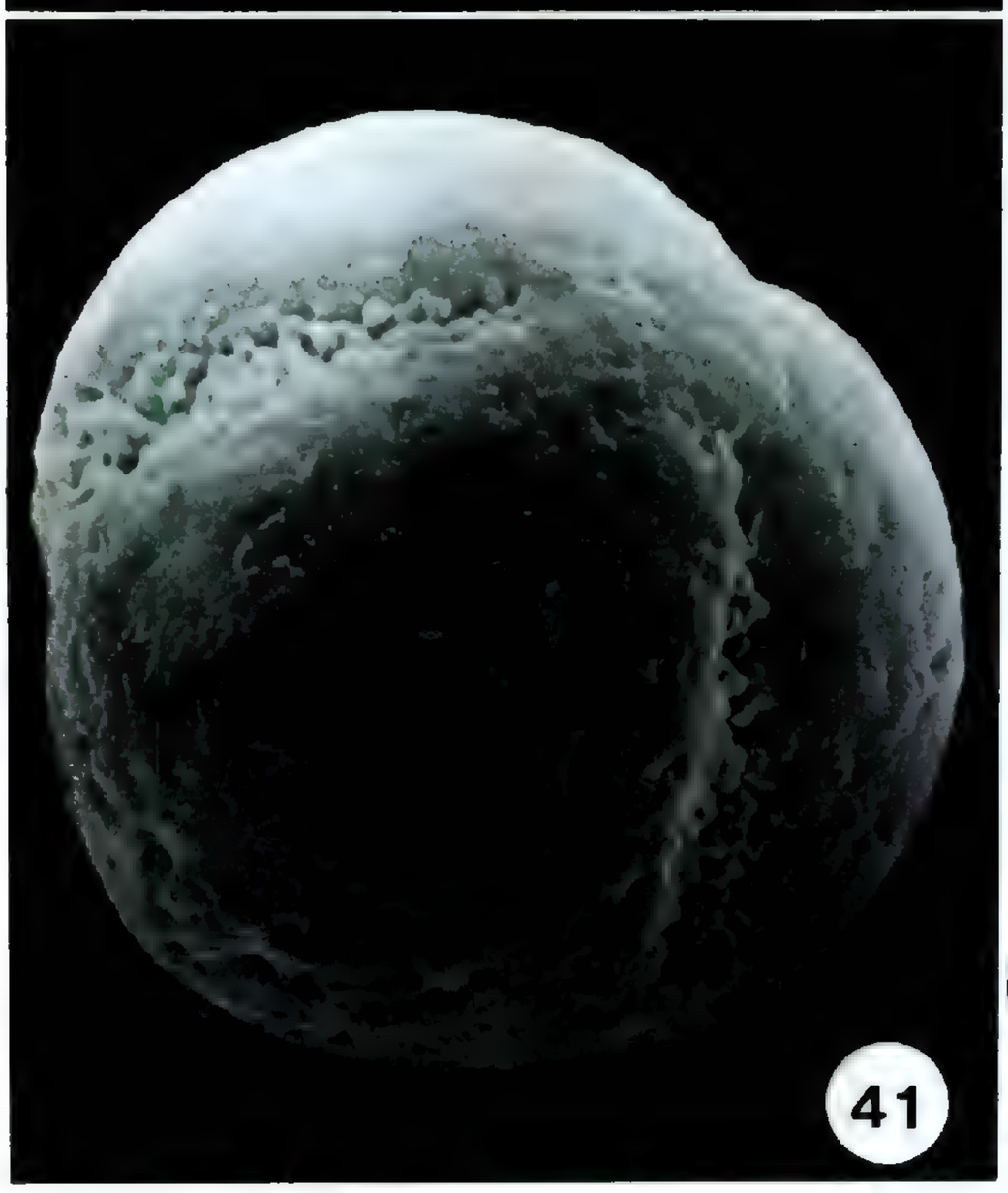




FIGURES 33–38.—33. Scanning electron micrograph of *Daphniphyllum calcinum*; ×2,200.—34. Transmission electron micrograph of *D. calycinum* showing tectate-columellate wall structure, footlayer, and endexine that thickens in apertural region (En); also note tectal perforations (small arrow); ×7,000.—35. Scanning electron







FIGURES 39–42.—39. Scanning electron micrograph of *Daphniphyllum himalayense*; ×3,200.—40. Transmission electron micrograph of *D. himalayense* showing tectate-columellate wall structure, thin footlayer, tectal perforation (small arrow) and endexine (En); ×25,500.—41. Scanning electron micrograph of *D. laurinum*; ×6,000.—42. Transmission electron micrograph of *D. laurinum* showing tectal perforation (small arrow), aperture region (A) with thickened endexine (En); ×15,540.

at times, is discontinuous and thickens somewhat in the apertural region (Fig. 69).

Fagaceae (6–8 genera, 800 species). The family has a cosmopolitan distribution. It is usually separated into three subfamilies.

Castaneoideae. The pollen is tricolporate, prolate, and averages 17 μm in polar diameter and 11 μm in equatorial diameter. Exine sculpturing is striate. The wall structure is tectate-columellate with a well-developed footlayer, the

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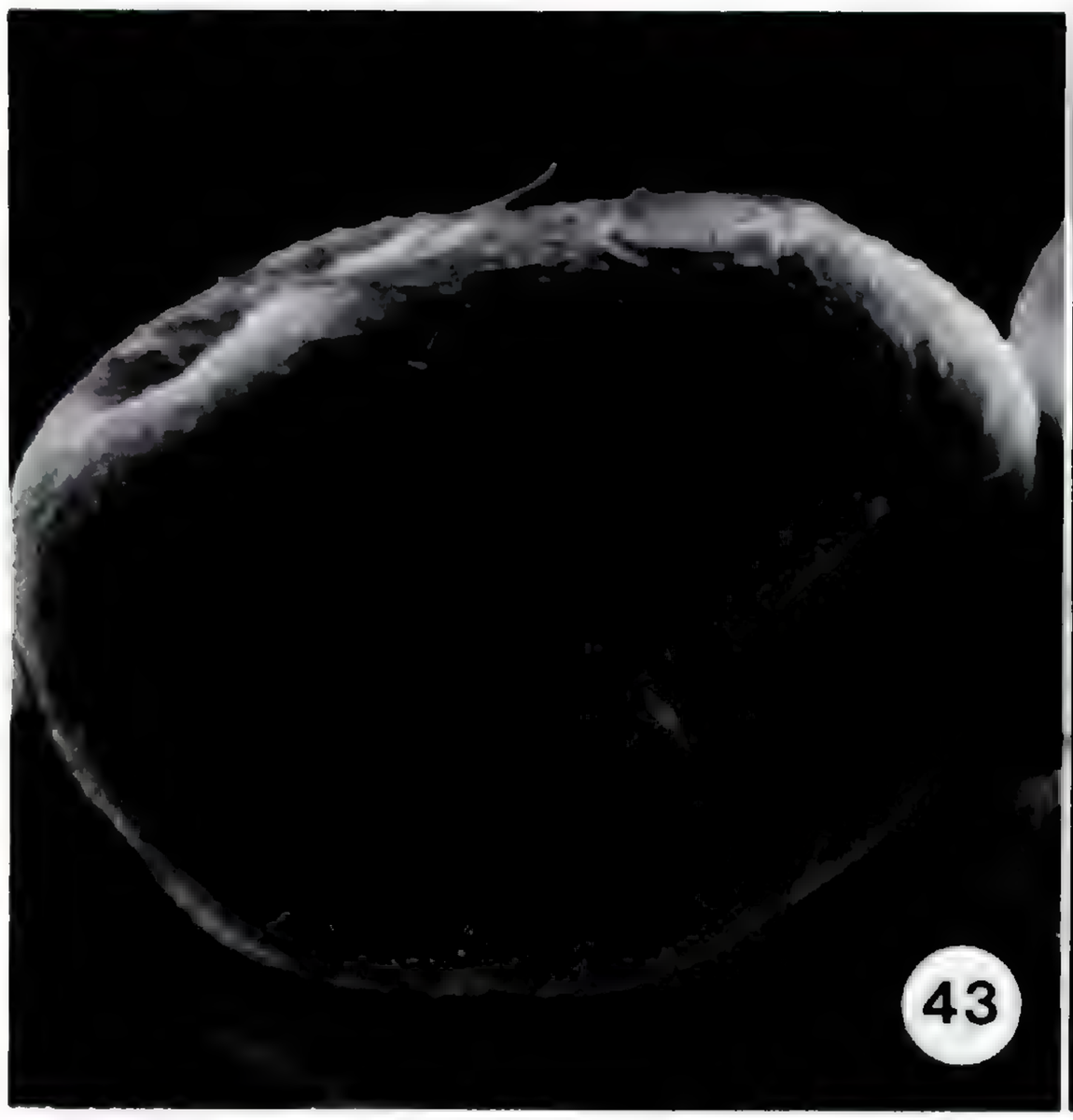
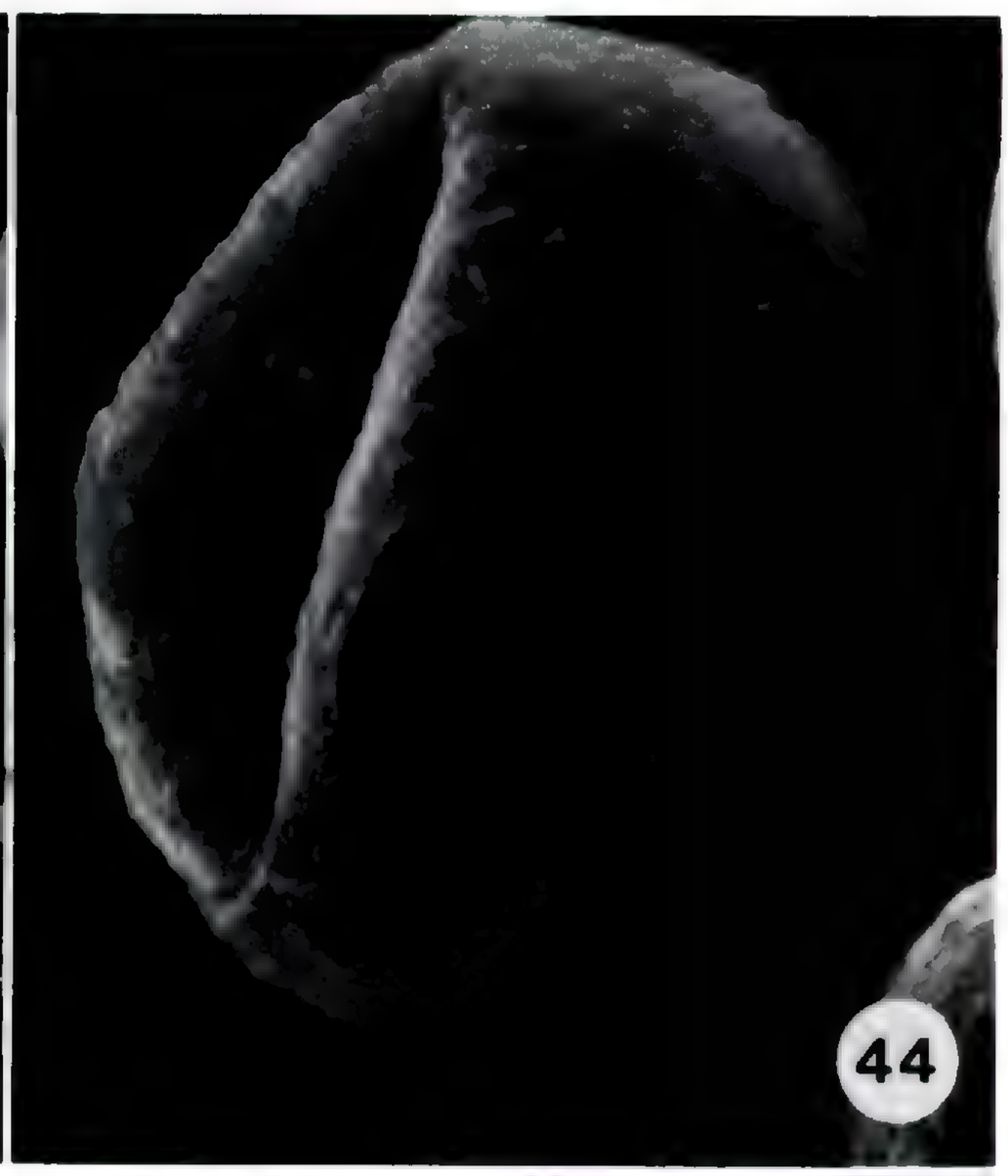
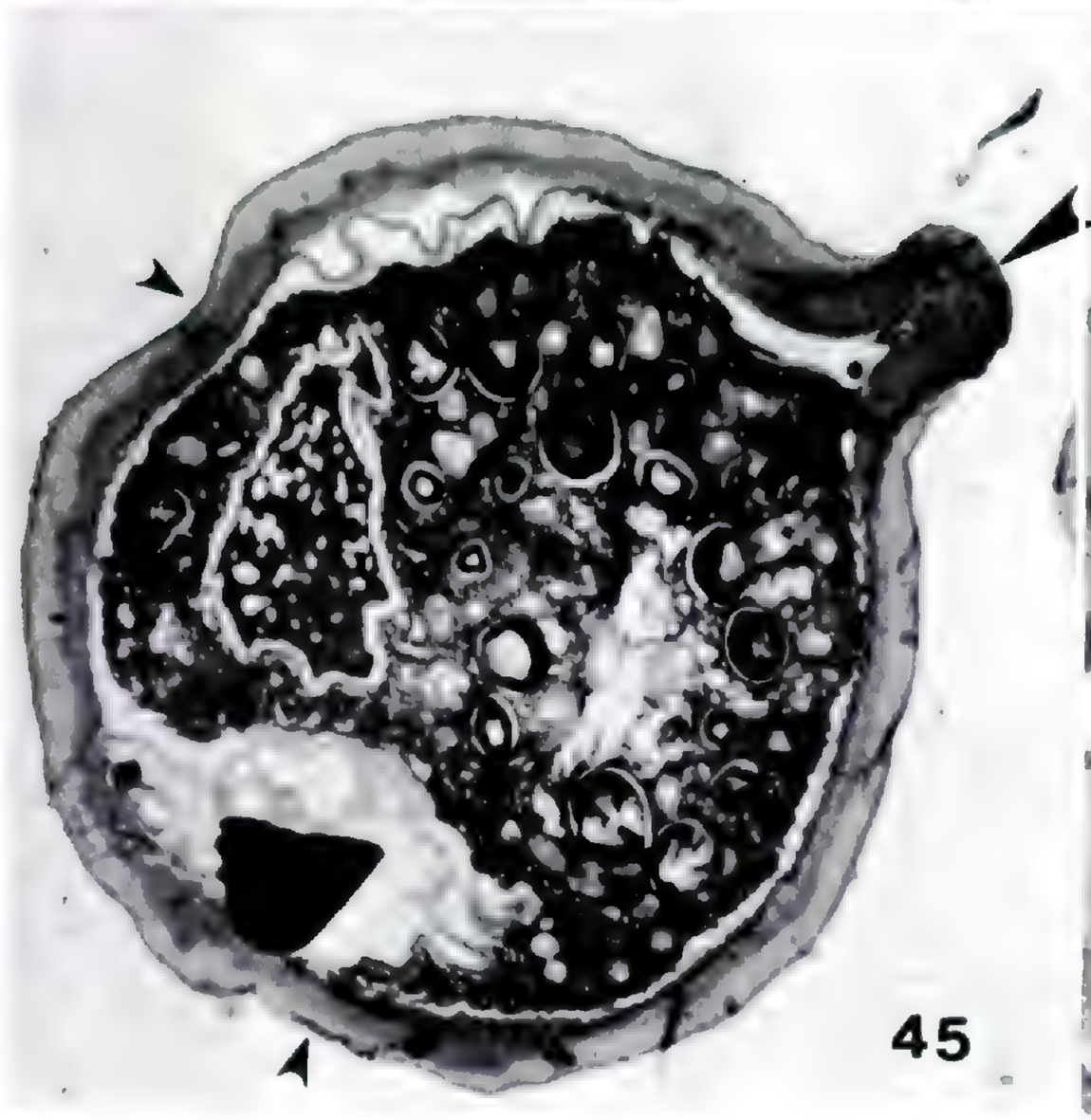
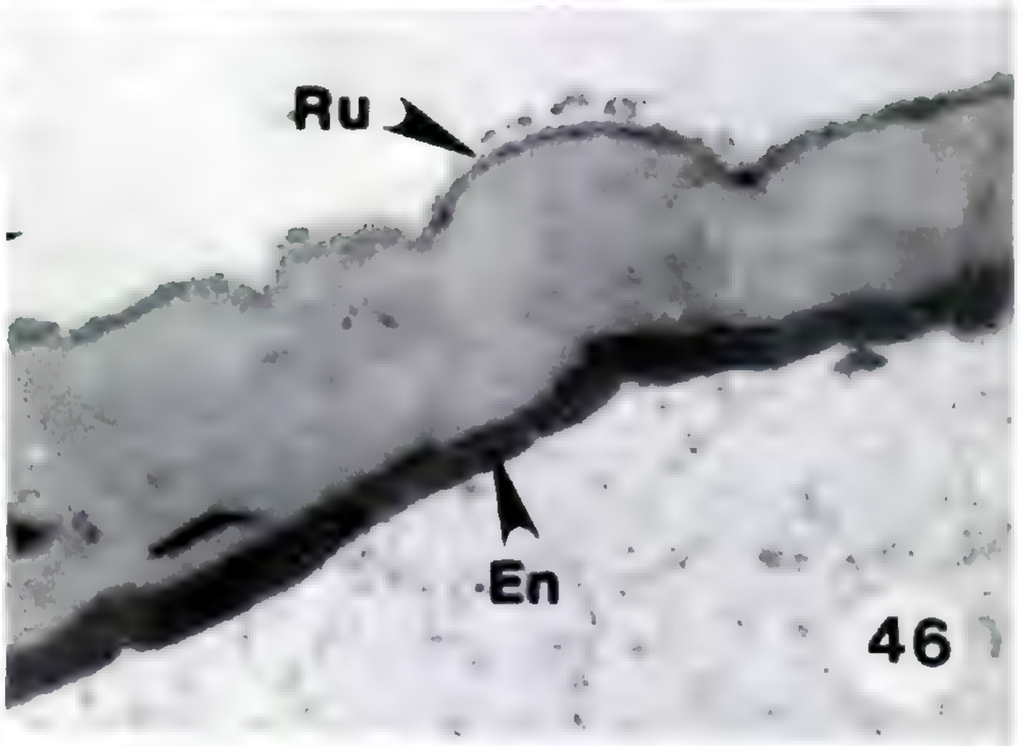
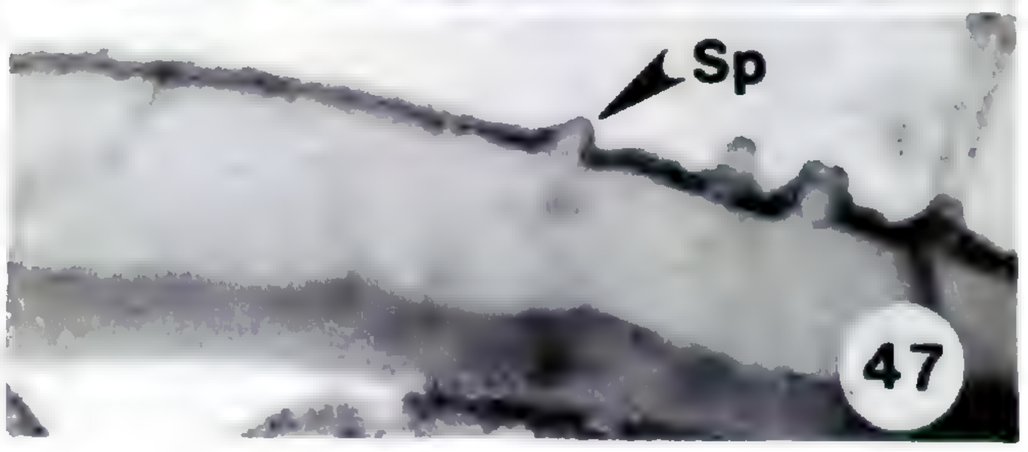
micrograph of *D. gracile*; ×2,900.—36. Transmission electron micrograph of *D. gracile* showing thin endexine in non-apertural region and a tectal perforation (small arrow); ×8,500.—37. Scanning electron micrograph of *D. neilgherrense*; ×3,200.—38. Transmission electron micrograph of *D. neilgherrense* showing aperture region (A) with endexine (En); ×10,000.











FIGURES 43–47.—43. Scanning electron micrograph of *Eucommia ulmoides* showing the colpus that narrows in the equatorial region; ×3,000.—44. Scanning electron micrograph of *E. ulmoides* showing straight, slit-like colpi; ×3,000.—45. Transmission electron micrograph of *E. ulmoides* showing atectate ektexine underlain by endexine, bulging colpus (large arrow), and the thinning of the ektexine in the slit-like apertures (small arrows); ×3,000.—46. Transmission electron micrograph of *E. ulmoides* in the hemisphere with slit-like apertures showing atectate wall, endexine (En), and rugulate (Ru) sculpturing (compare to Fig. 44); ×15,000.—47. Transmission electron micrograph of *E. ulmoides* in the region of the colpus that narrows equatorially showing small spinules (Sp) and wall structure; ×10,000.

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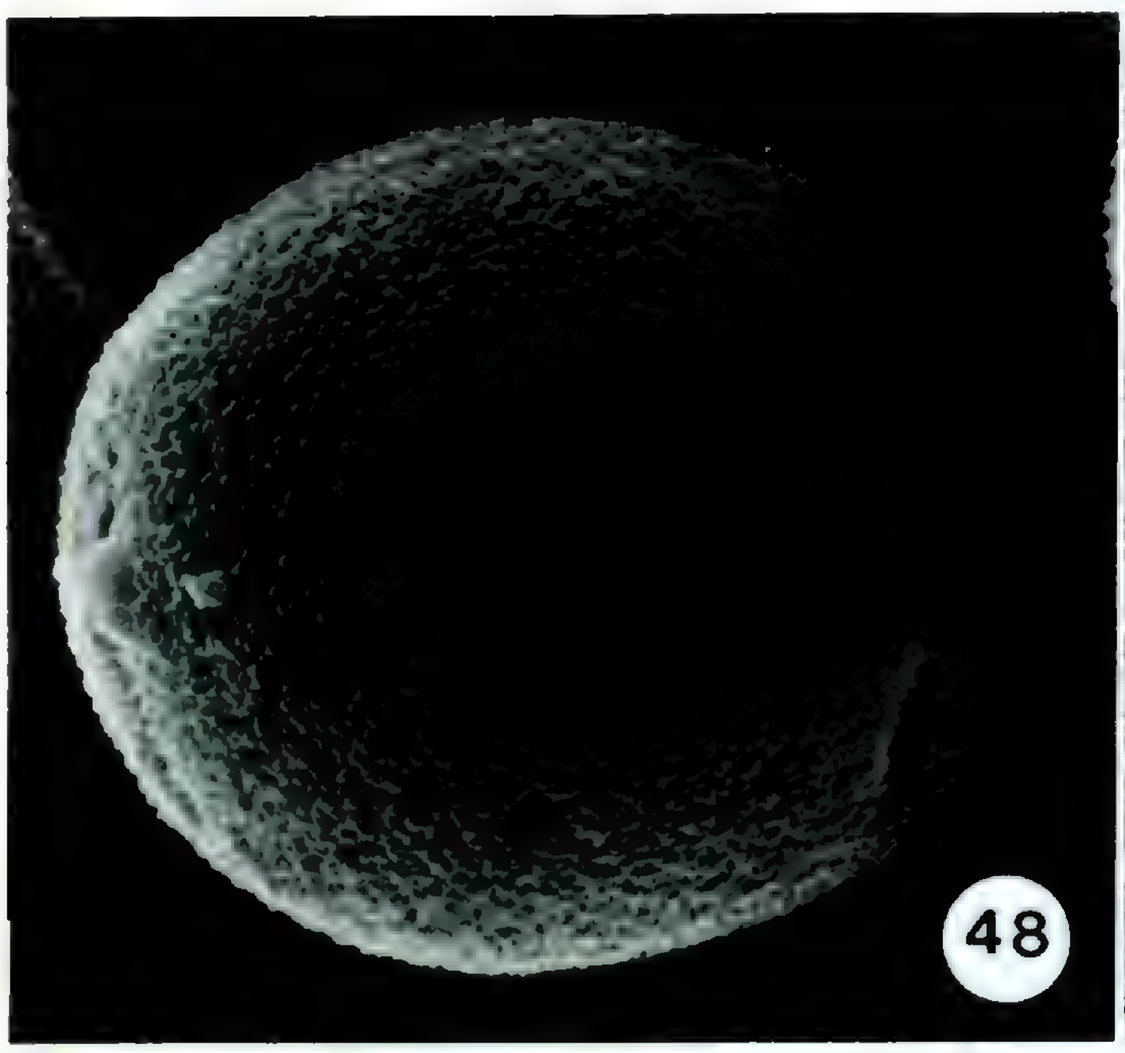
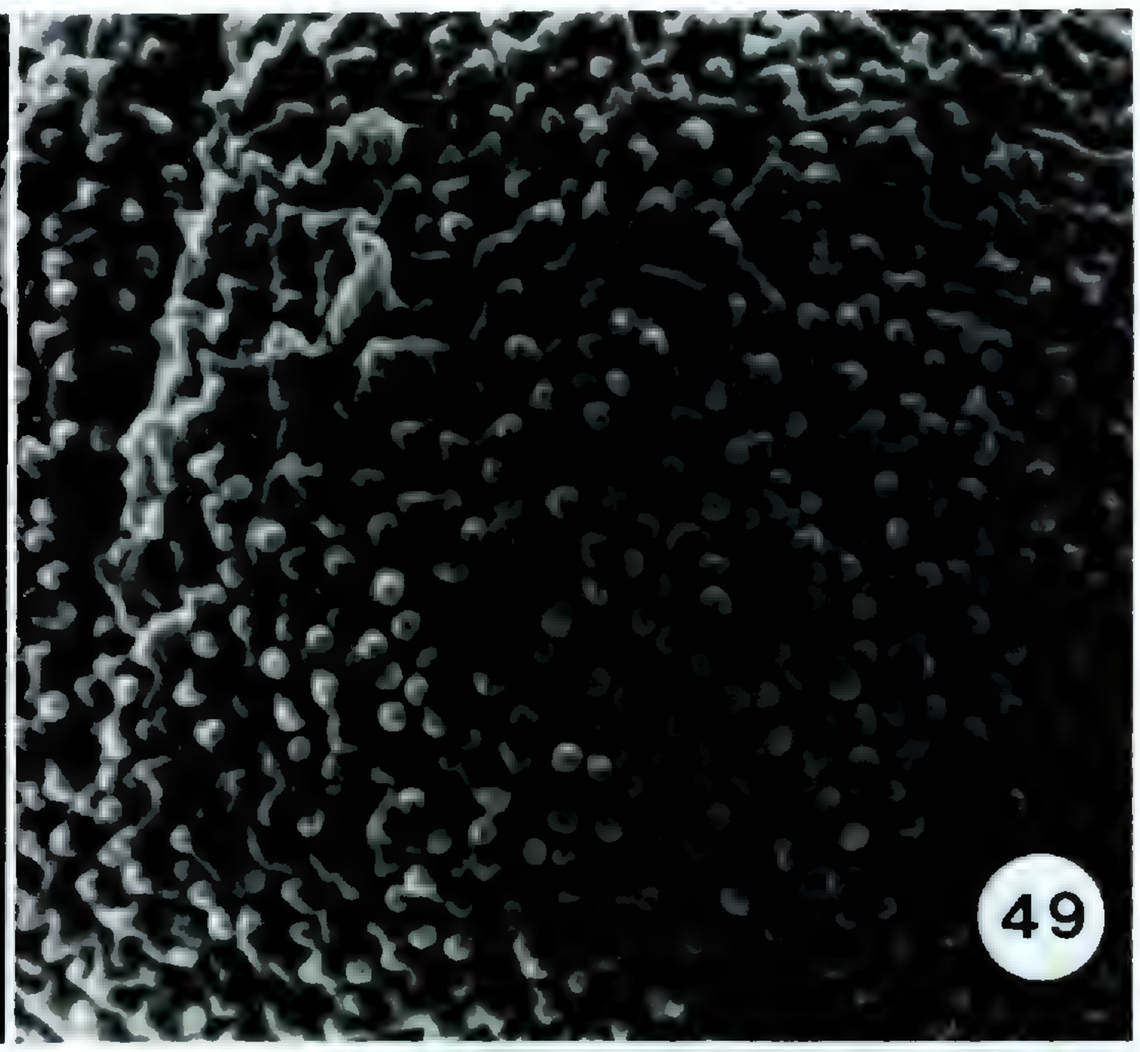
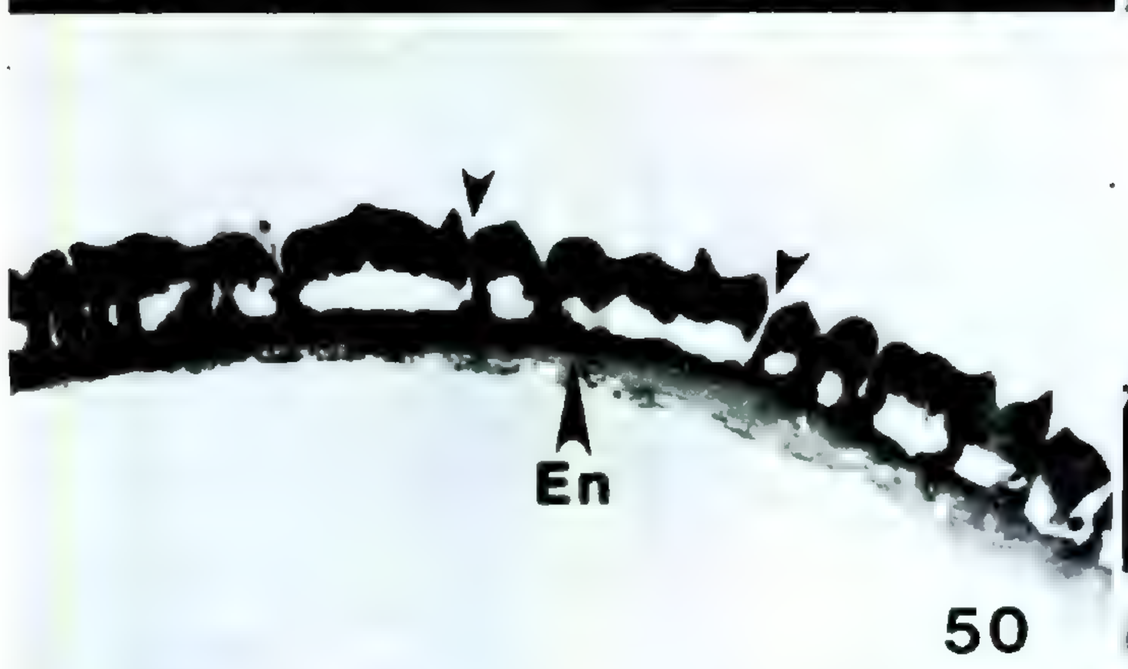
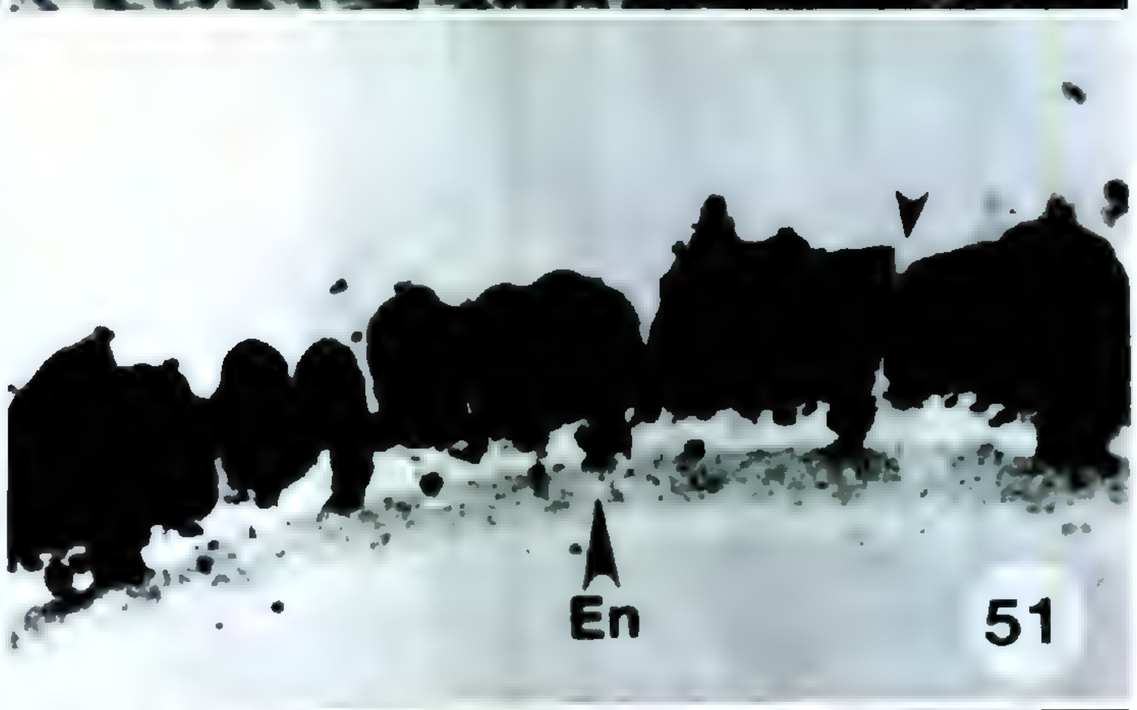
FIGURES 48–53.—48. Scanning electron micrograph of *Leitneria floridana*; ×2,400.—49. Scanning electron micrograph of *L. floridana* showing exine sculpturing; ×6,400.—50. Transmission electron micrograph of *L. floridana* showing tectate-columellate wall structure, thin footlayer, endexine (En), and tectal perforation (small









arrows); ×8,500.—51. Transmission electron micrograph of *Barbeya oleoides* showing thick tectum with small (micro-) perforations (small arrow), lack of footlayer, and thick endexine (En); ×22,520.—52. Scanning electron micrograph of *B. oleoides*; ×3,500.—53. Scanning electron micrograph of a collapsed pollen grain of *B. oleoides* showing trirudiate thick region in the polar region; this characteristic is reminiscent of some fossil normapolles dispersed pollen types; ×3,200.

tectum is traversed by small perforations. A thin endexine underlies the ektexine in nonapertural regions but thickens considerably in apertural regions (Crepet & Daghlian, 1980; Miyoshi, 1983).

Fagoideae. The pollen is tricolporate in *Fagus* and stephanocolpate in *Nothofagus,* and is spherical-oblate (*Fagus*) to oblate (*Nothofagus*). *Fagus* pollen is about 37 μm in polar diameter and 38 μm in equatorial diameter; that of *Nothofagus* is about 20 μm in polar diameter and 32 μm in equatorial diameter. Exine sculpturing in *Fagus* pollen consists of minute striations. Pollen of *Nothofagus* has widely spaced spines. Pollen wall structure of *Fagus* is tectate-columellate with a well-developed footlayer, the tectum is traversed by small perforations. A well-developed endexine, which thickens in the apertural regions, is also evident. Pollen wall structure of *Nothofagus* is tectate-granular with a relatively thick footlayer that is underlain by a well-developed endexine. The endexine becomes thicker in the apertural regions. The tectum is imperforate (Crepet & Daghlian, 1980; Praglowski, 1981, 1982).

Quercoideae. The pollen is tricolporate, prolate to spheroidal, about 28 μm in polar diameter. The exine sculpturing is scabrate to rugulate, the wall structure is tectate-columellate with a thick footlayer that is underlain by an endexine. The endexine thickens in the apertural regions (Smit, 1973; Crepet & Daghlian, 1980; Solomon, 1983a, 1983b).

Betulaceae (6 genera, 120 species). This family is distributed primarily in temperate regions of the Northern Hemisphere. Pollen is triporate (*Betula, Ostrya, Corylus, Ostryopsis, Carpinus*) to stephanoporate (*Alnus*), oblate, 20–30 μm in equatorial diameter. Exine sculpturing is minutely scabrate to slightly rugulate (Fig. 66; Erdtman, 1952; Adams & Morton, 1972; Kedves, 1979; Crane, pers. comm.), the wall structure is tectate-granular (Fig. 67; Erdtman, 1969; Rowley, 1981; Rowley & Prijanto, 1977; this study); however, columellate-like structures are often present in the infrastructural layer. (Dunbar & Rowley, 1984). The tectum is traversed by minute channels (Fig. 67). The footlayer is underlain by a very thin endexine that does not thicken in the apertural regions in *Corylus*; however, in *Betula* it thickens somewhat and is separated from the footlayer to form an atrium.

CASUARINALES

Casuarinaceae (1–2 genera, 50 species). This family is native to some southeast Pacific islands,

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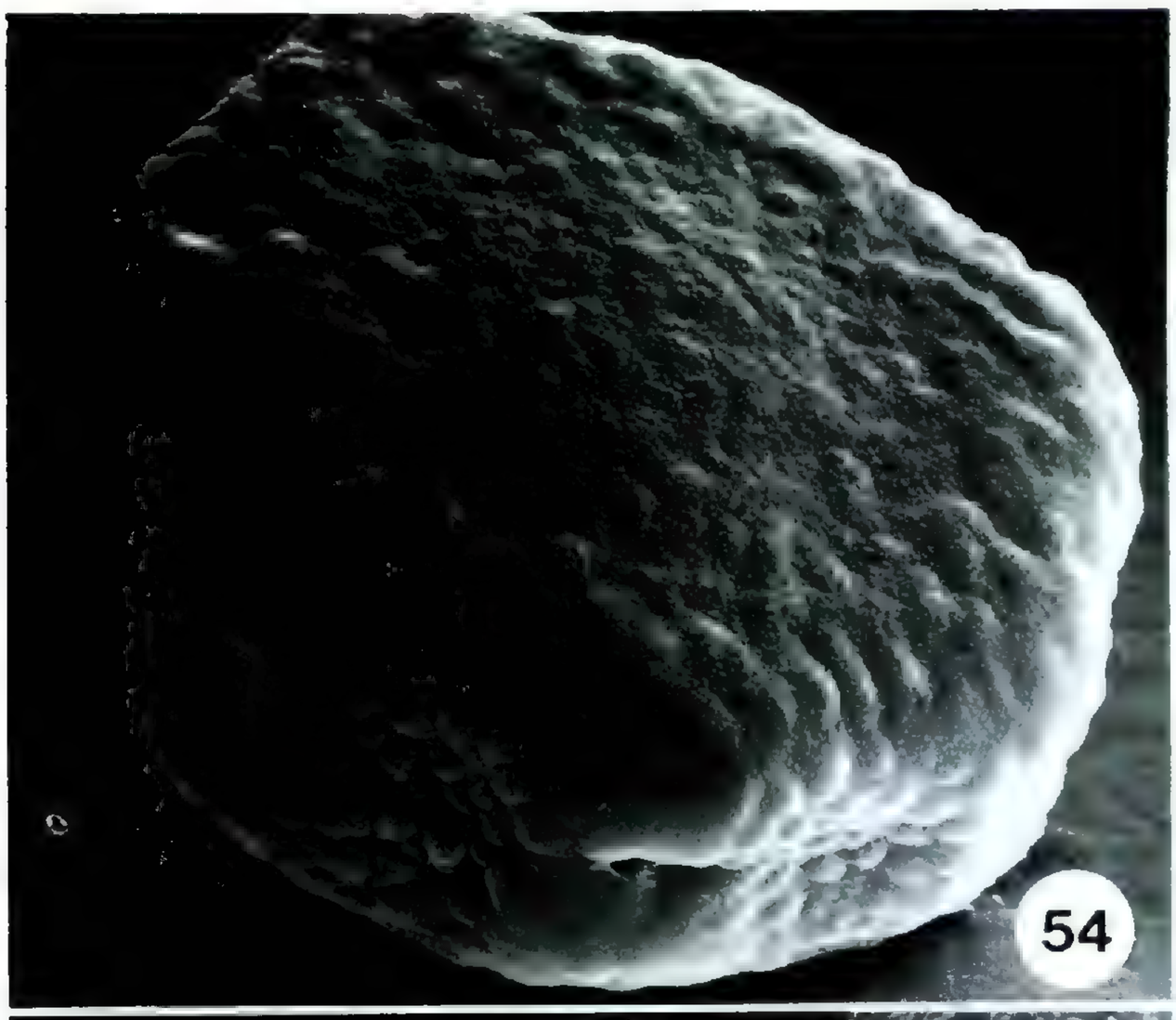
FIGURES 54–59.—54. Scanning electron micrograph of *Ulmus glabra*; ×1,840.—55. Transmission electron micrograph of *U. glabra* showing thin tectum, granular infrastructure, and thin footlayer; ×4,500.—56. Scanning electron micrograph of *Celtis talla*; ×3,310.—57. Transmission electron micrograph of *C. spinosa* showing tectum, infrastructure, and thin footlayer; ×7,100.—58. Scanning electron micrograph of *Cannabis sativa*; ×2,900.—59. Transmission electron micrograph of *C. sativa* showing tectum, granular infrastructure, and thin footlayer. A thin, less dense layer is sometimes evident in this taxon (endexine); ×10,260.

FIGURES 60–67.—60. Scanning electron micrograph of *Casuarina stricta*; ×1,500.—61. Transmission electron micrograph of *C. stricta* showing thick tectum with minute channels (small arrows), granular infrastructure, and thin footlayer; ×10,094.—62. Scanning electron micrograph of *Gymnostoma deplancheanum*; ×2,000.—63. Transmission electron micrograph of *G. deplancheanum* showing tectate-granular wall structure; ×6,840.—64. Scanning electron micrograph of *Myrica asplenifolia*; ×2,900.—65. Transmission electron micrograph of *M. asplenifolia* showing minute tectal channels (small arrows), granular-columellate infrastructure, and footlayer; ×15,540.—66. Scanning electron micrograph of *Betula alba*; ×2,900.—67. Transmission electron micrograph of *B. alba* showing minute tectal channels (small arrow) and granular infrastructure; ×18,960.

FIGURES 68–73.—68. Scanning electron micrograph of *Balanops vitiense* showing spinulose exine sculpturing; ×3,400.—69. Transmission electron micrograph of *B. vitiense* showing minute tectal perforations (small arrows), granular to columellate infrastructure, discontinuous footlayer, and dark-staining endexine (unacetolyzed pollen grain); ×15,540.—70. Scanning electron micrograph of *Pistacia terebinthus* showing porate (ulceroid-like) apertures, finely reticulate tectum with small scabrae; ×2,500.—71. Transmission electron micrograph of *P. terebinthus* showing tectate-columellate wall structure and thick footlayer; ×12,500.—72. Pollen of *Populus deltoides.* (a) Transmission electron micrograph of whole grain showing ektexinal interruptions that may represent small, ulceroid-like pores (arrows); ×4,500. (b) Transmission electron micrograph showing tectate-columellate wall structure and very thin footlayer; ×18,500.—73. Transmission electron micrograph of *Dorstenia* showing tectal perforations (arrows) and granular infrastructure; ×21,000.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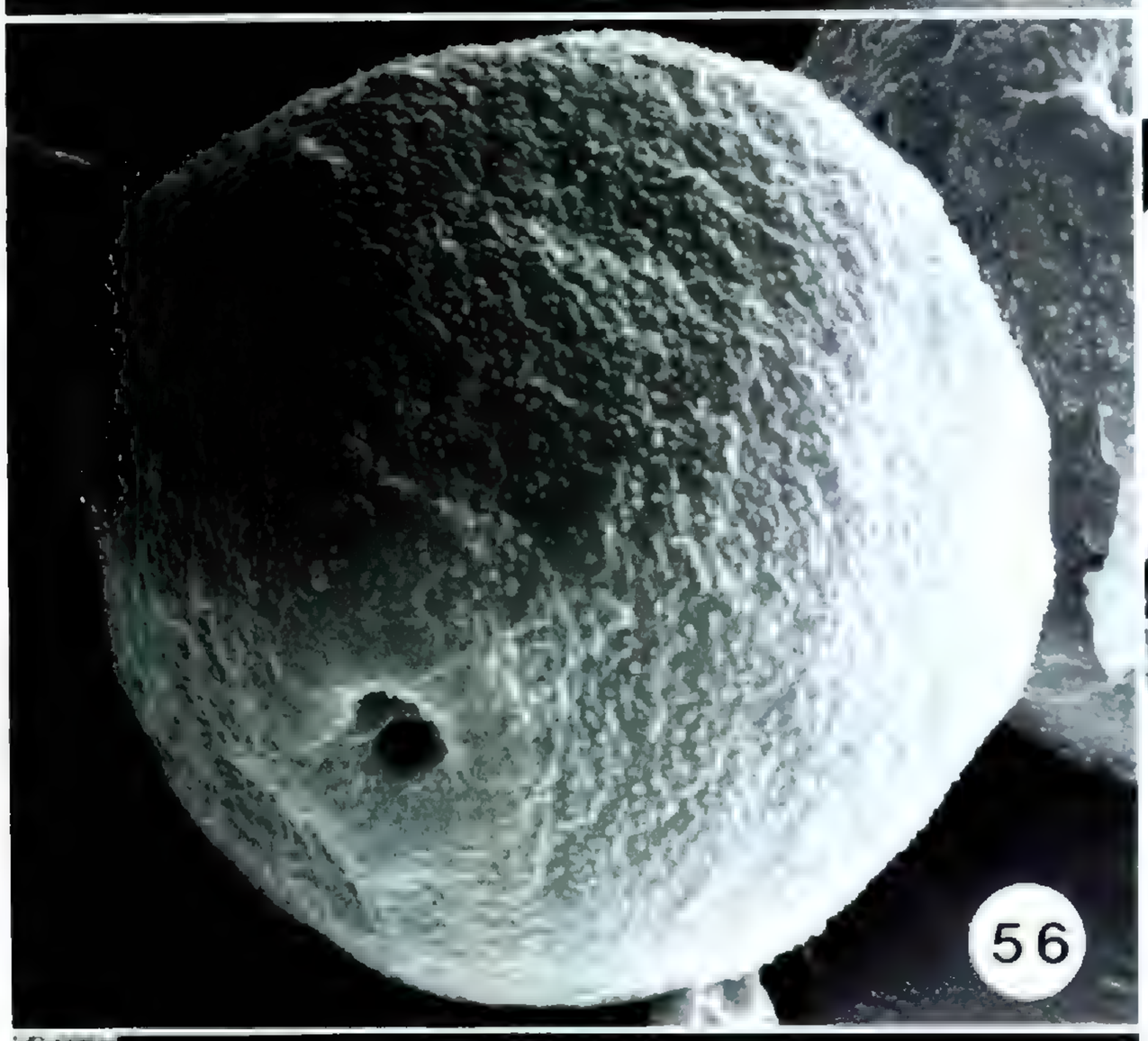
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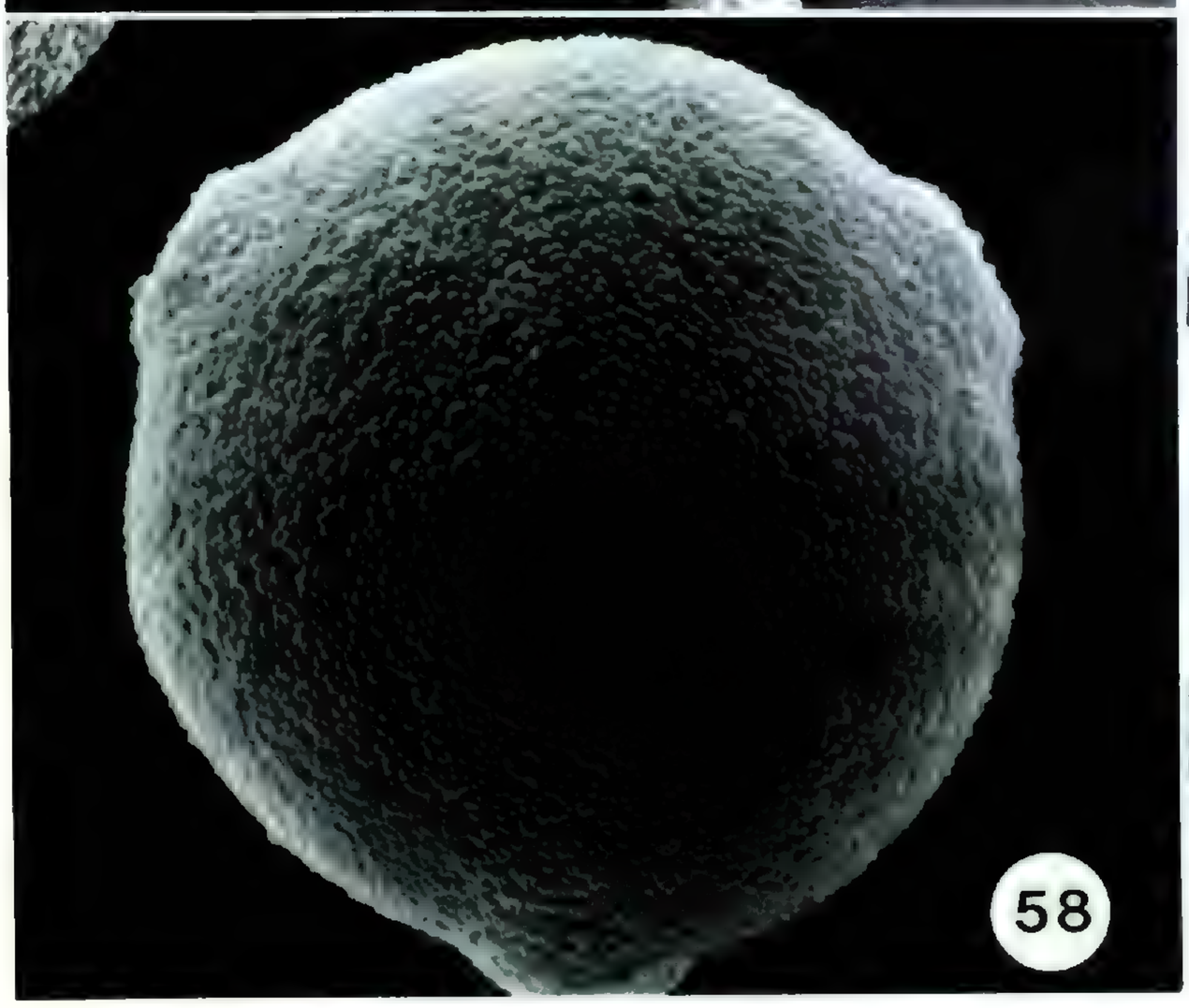
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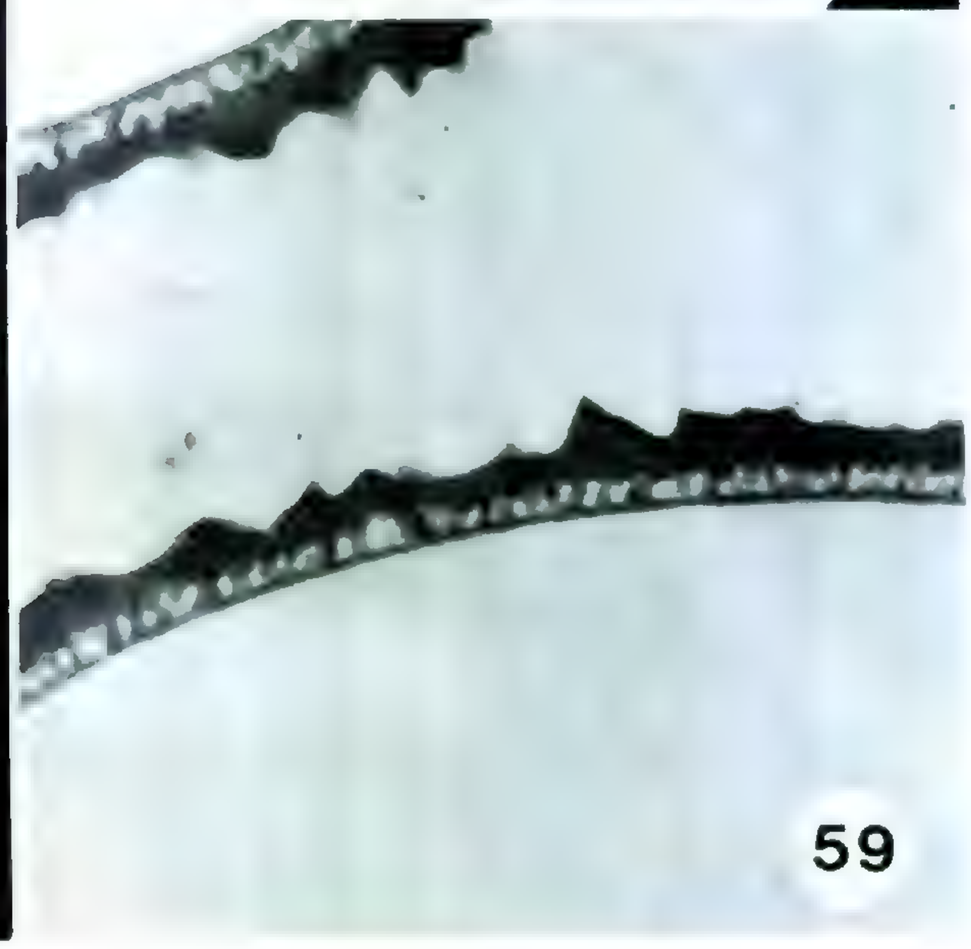
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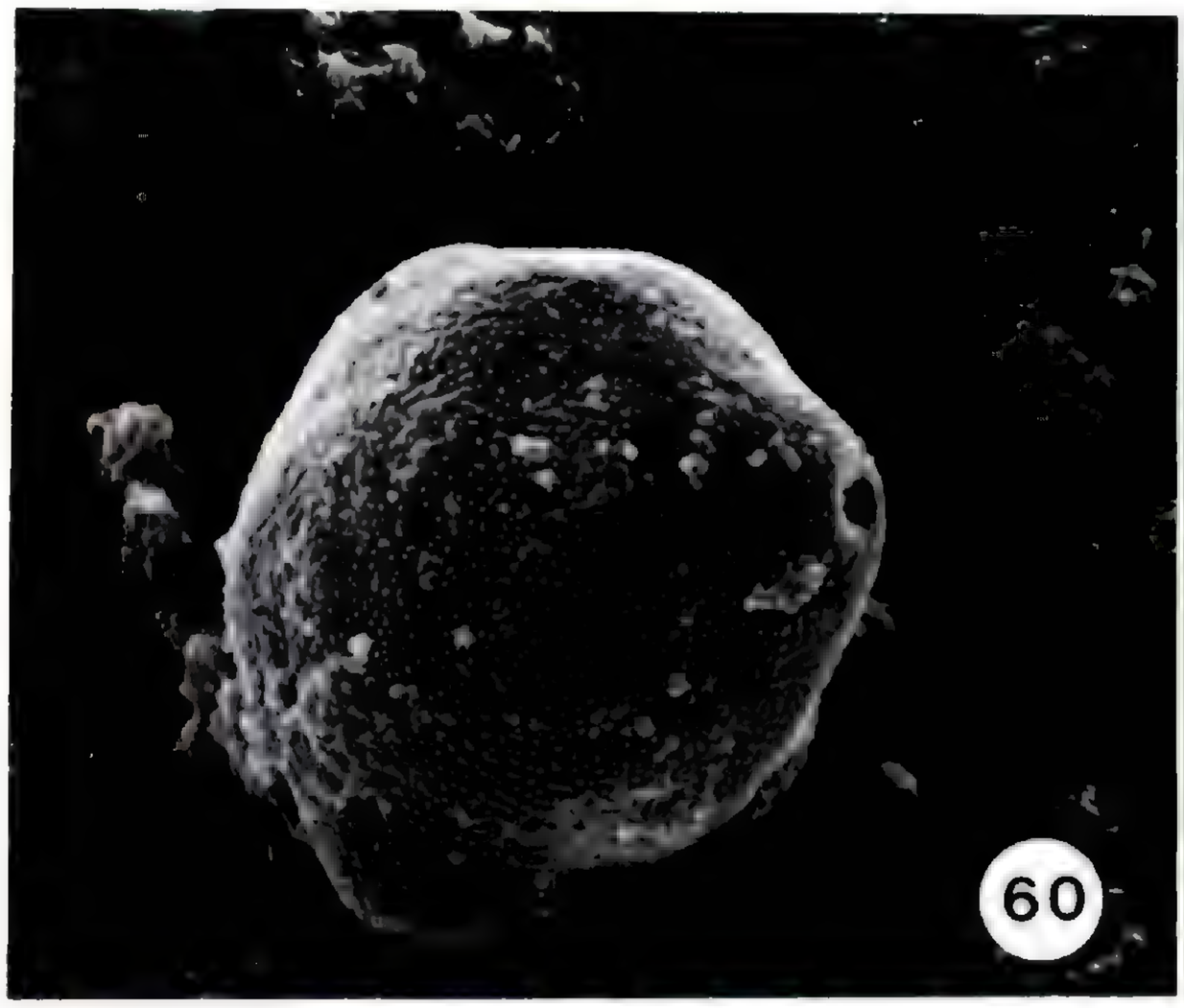
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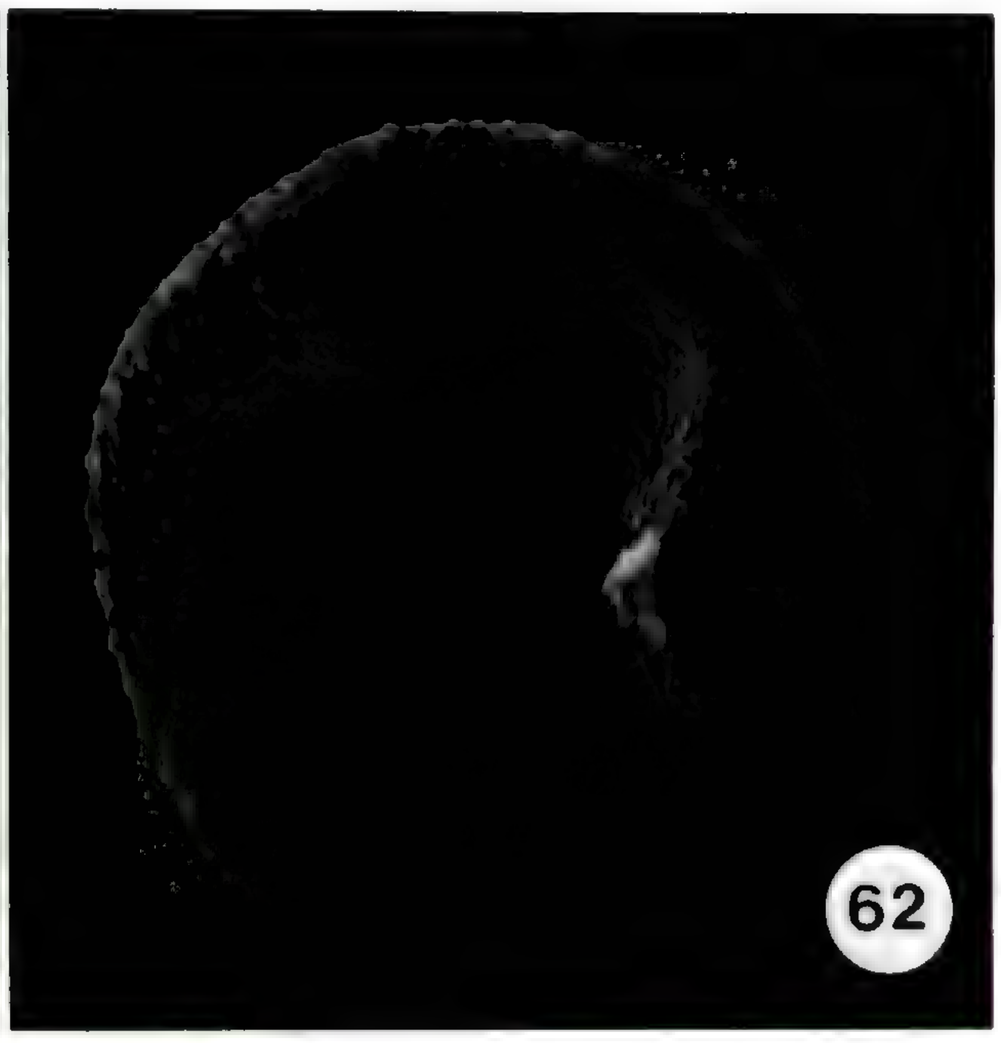
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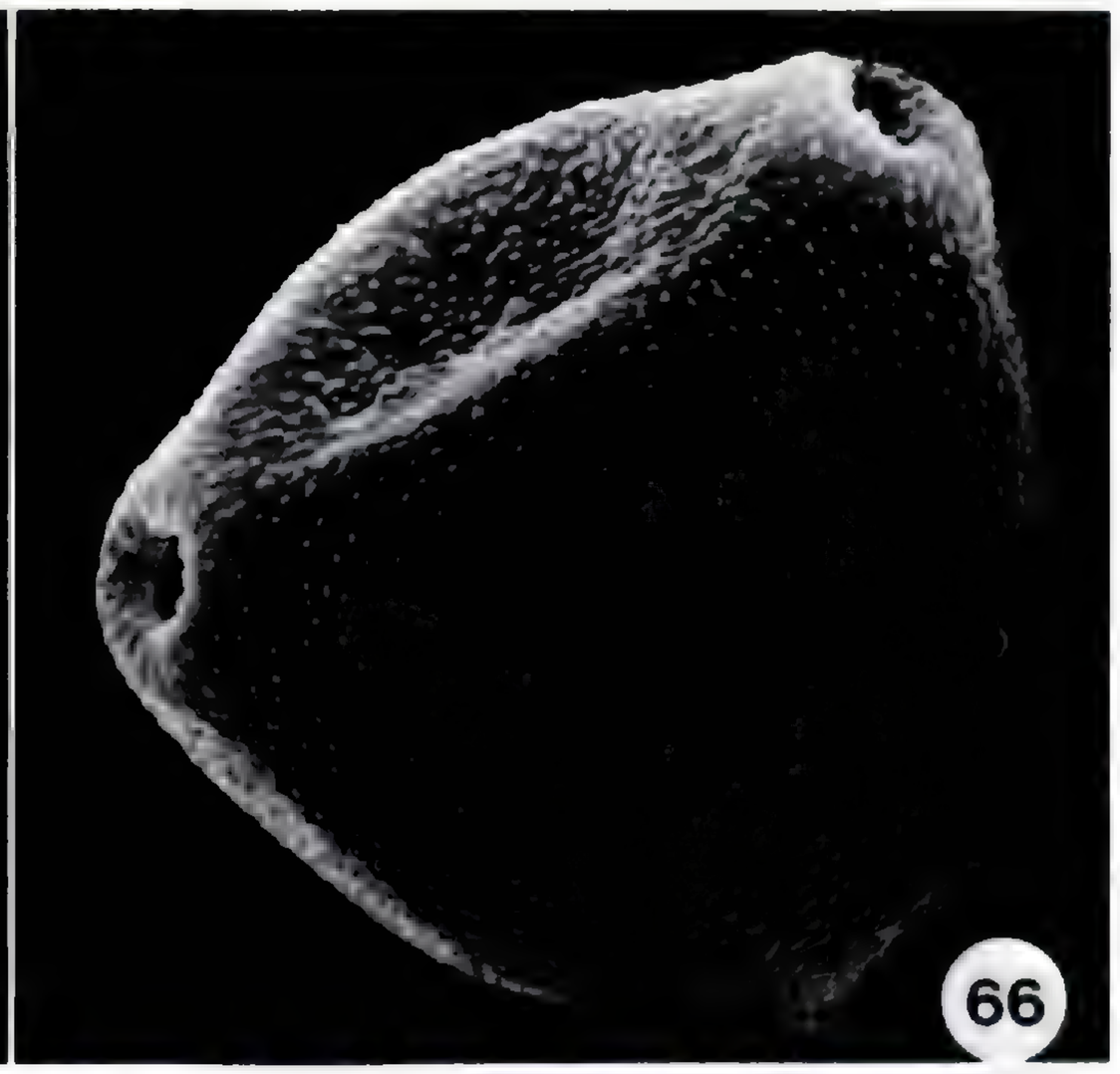
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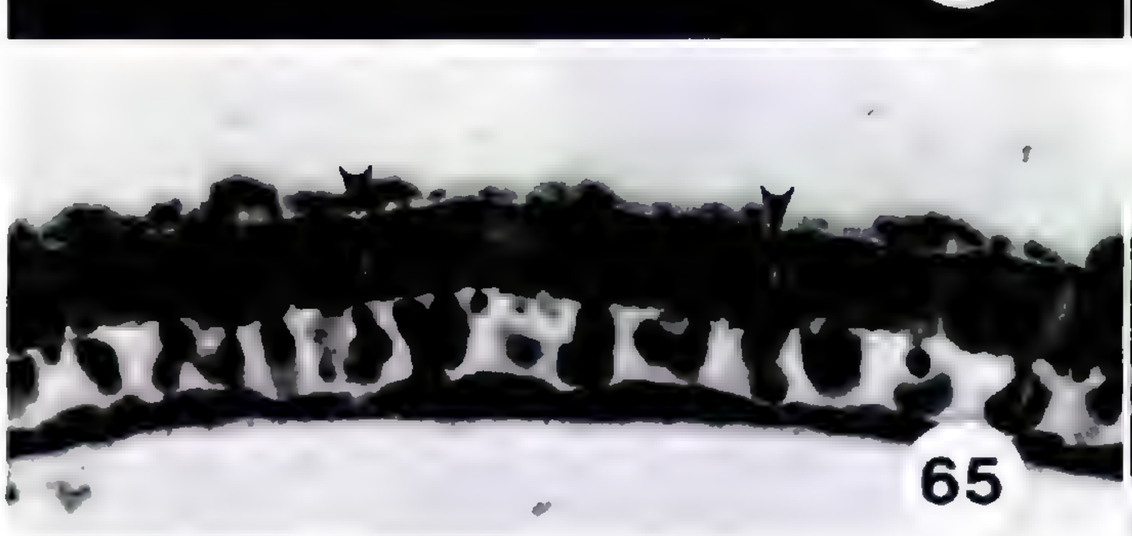
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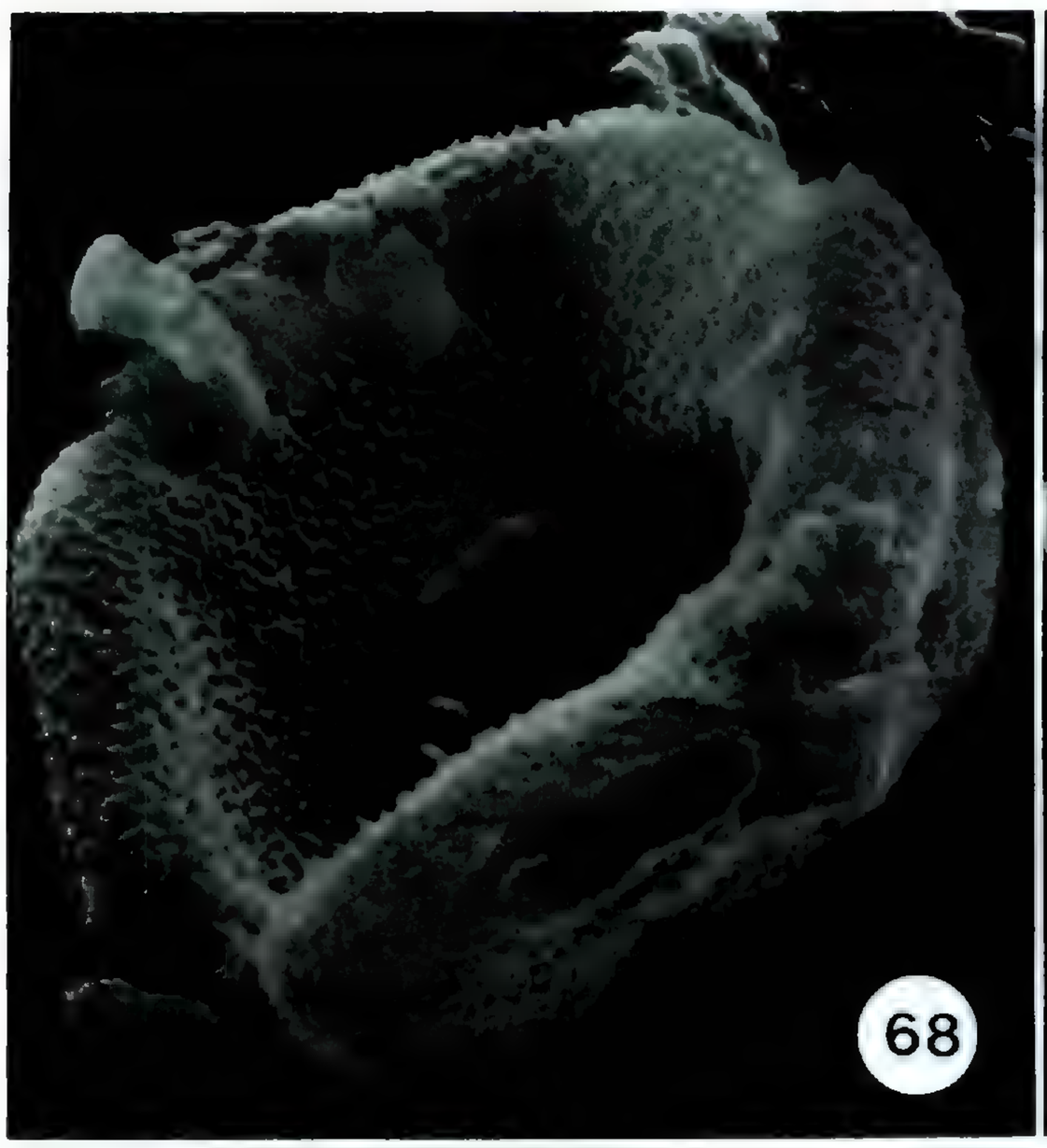
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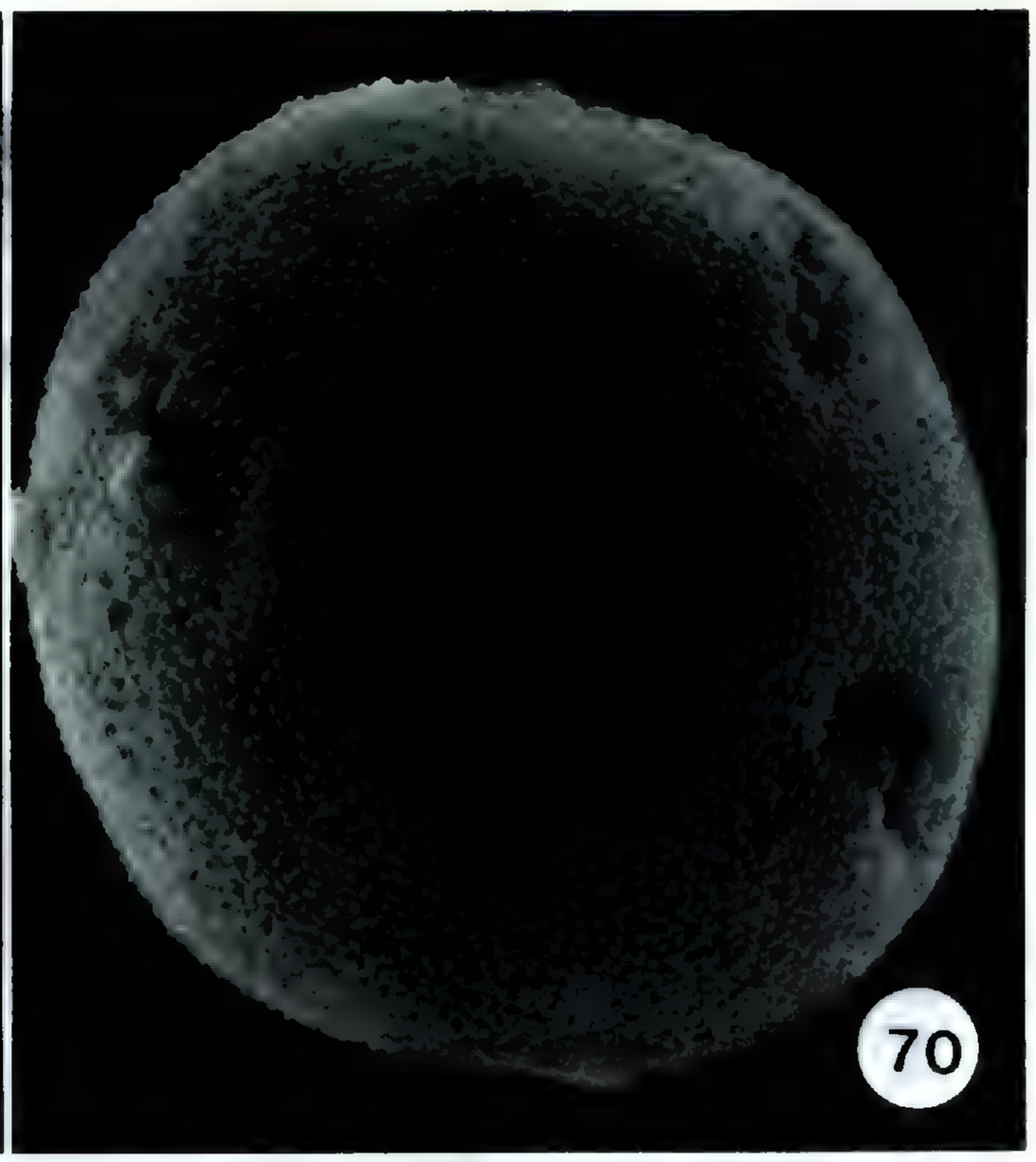
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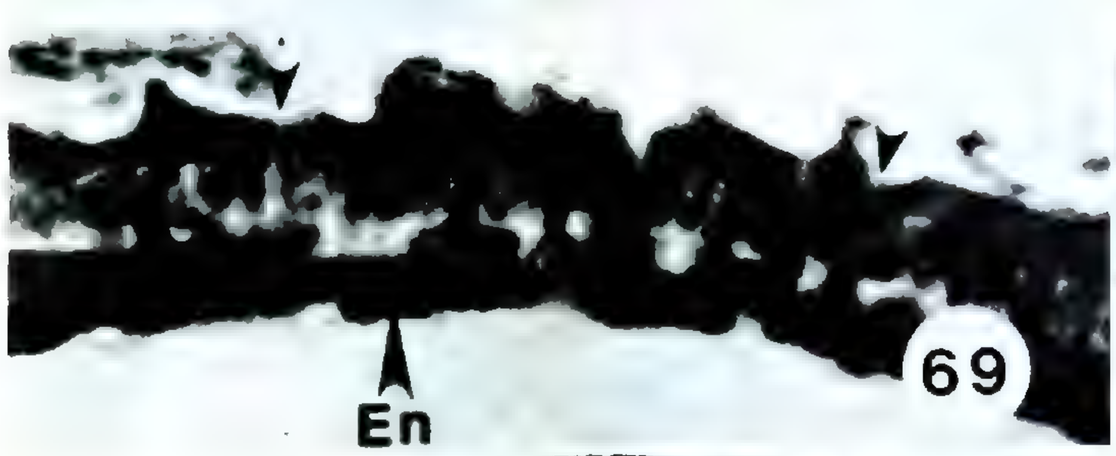
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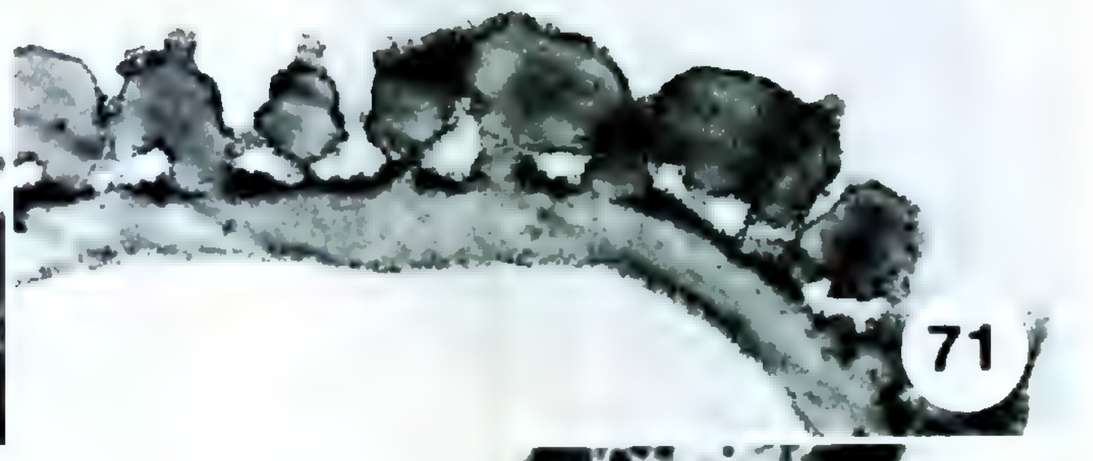
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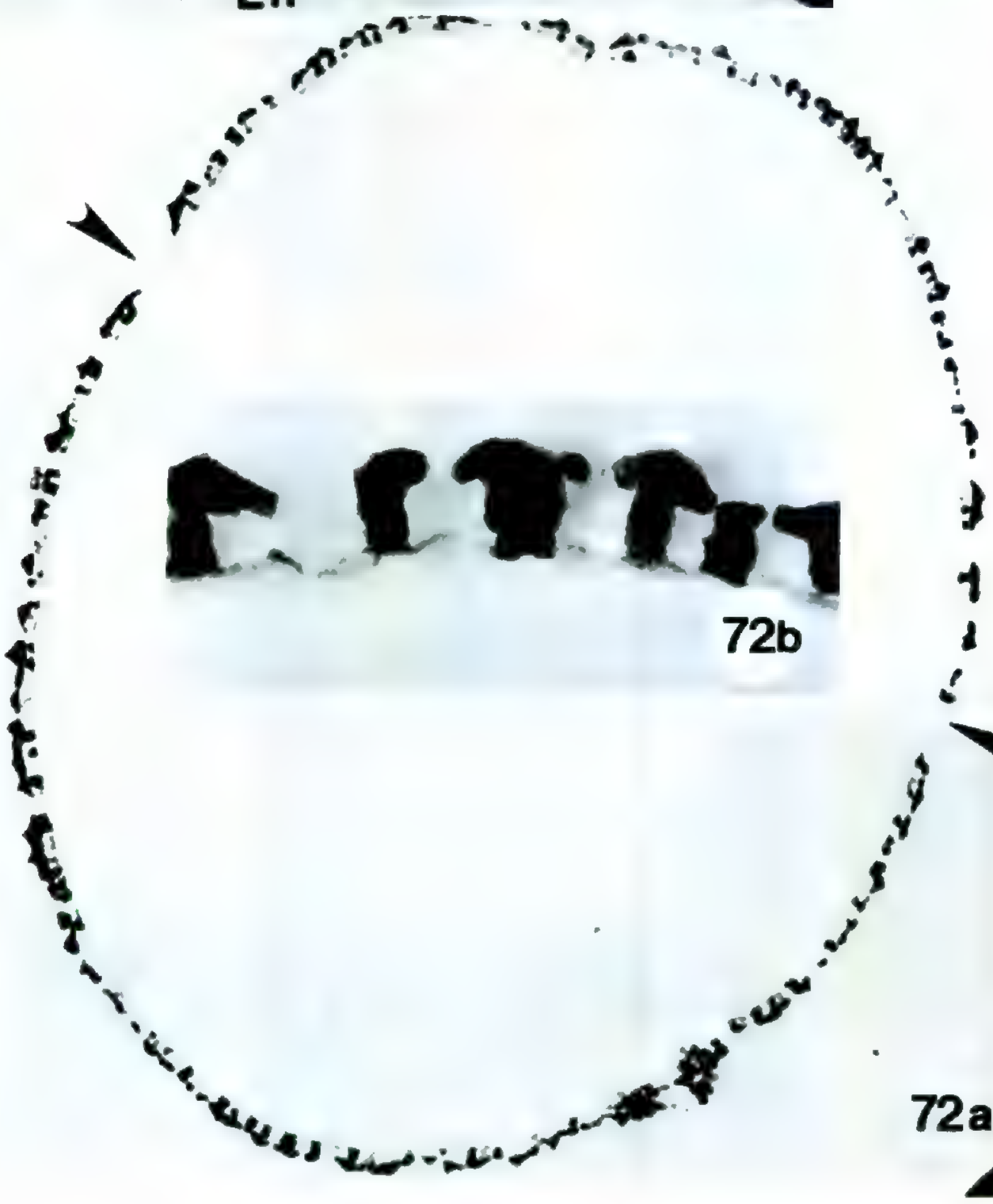
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New Guinea, Sumatra, and Australia. The pollen is triporate, oblate, averaging 29 μm in equatorial diameter (Kershaw, 1970) and 23 μm in polar diameter (Figs. 60, 62). Exine sculpturing consists of small spinules or scabrae and sometimes appear rugulate, the wall structure of *Casuarina* is tectate-granular (Figs. 61, 63), the thick tectum is traversed by minute channels (Fig. 61). A thin footlayer is present that separates from the granular layer in the apertural region to form an atrium. No endexine is evident, but Coetzee and Praglowski (1984) reported a thin endexine in the eight species they investigated. Pollen wall structure in *Gymnostoma* is identical to that in *Casuarina*; however, the footlayer remains in contact with the granular layer in the apertural region (this study).

POLLEN CHARACTERS USED IN THE ANALYSES

The pollen characters chosen for the phylogenetic and similarity cluster analysis of Hamamelidae are those that vary among the taxa investigated. Characters that are present but do not vary are excluded. The characters are of two types: (a) those that are present (1) or absent (0) and no other variation of the character exists, and (b) those that are present (1) or absent (0) and a dependent associated character state also exists that can thus be determined to be present or absent, for example, pollen shed in monads; if pollen is shed in some other unit, the monad character is scored absent (0) and the character state it possesses (e.g., tetrads) is scored present (1). Thirty character states that vary are recognized for pollen of the Hamamelidae (see legend Appendix II). The character states are discussed below, in addition to their association with taxonomic units above the generic level.

POLLEN UNIT (TWO CHARACTER STATES)

All species of Hamamelidae shed their pollen in monads except Myrothamnaceae, which shed pollen in tetrads.

POLLEN SHAPE (THREE CHARACTER STATES)

Pollen shape (prolate, spherical, oblate) varies considerably among species, genera, and families. Taxa with equatorially placed colpi are predominantly prolate to spherical (e.g., Trochodendrales, Hamamelidales). Taxa with equatorially positioned pores are usually oblate (e.g., Juglandales, Casuarinales), and taxa with peri-porate or -colpate pollen are generally spherical (e.g., Liquidambaroideae). If any species varies between two or three of the shape classes, both or all shape characters are scored as present (1).

APERTURE TYPE (NINE CHARACTER STATES)

The predominant aperture type is tricolpate (e.g., Trochodendrales, Hamamelidales). The triporate and stephanoporate (greater than three equatorial-positioned pores) are common in the Juglandales, Myricales, Casuarinales, Ulmaceae, and Betulaceae. The pericolpate and periporate condition occurs in the Liquidambaroideae, Moraceae, and Urticaceae. Stephanocolpate pollen occurs in two taxa: *Balanops vitiensis* (A. C. Smith) Hjedruqvist and *Nothofagus* spp. The tricolporate type is restricted to the Fagales, Leitneriales, and possibly Rhoipteleaceae (Stone & Broome, 1971), and the Barbeyaceae. The diporate type is found in some Moraceae and the Celtidoideae.

SUPRATECTAL SCULPTURING (SIX CHARACTER STATES)

Exine sculpturing is highly variable in many plant groups, including the Hamamelidae. In the semitectate (reticulate) pollen of the Trochodendrales and Hamamelidales, the tectum is often psilate. Another easily recognizable tectal ornament is small spines or spinules. Spinules occur predominantly in the Juglandales, Casuarinales, Myricales, and Betulaceae. Scabrae occur in the Urticales and the rugulate-verrucate sculpturing type in Urticales, Juglandales, and Fagales. Clavate sculpturing occurs only in the Myrothamnaceae, and the striate type only in the Fagaceae (e.g., *Fagus, Castanea*).

WALL STRUCTURE

TECTUM (FOUR CHARACTER STATES)

Pollen of all taxa have a tectum except for *Myrothamnus*, which is intectate. The pollen wall structure of *Eucommia* is unique in having atectate pollen (cf. *Degeneria*). Semitectate (reticulate) pollen is easily recognizable with light microscopy and occurs in the Trochodendrales and Hamamelidales. In Daphniphyllales, Leitneriales, Barbeyaceae, and Fagaceae the tectum is more continuous and is traversed by microperforations discernable only by SEM. In some Ur-

ticales, Juglandales, Myricales, and Casuarinales the tectum appears imperforate with SEM; however, TEM reveals that the tectum is traversed by microchannels.

INFRASTRUCTURE (TWO CHARACTER STATES)

The infrastructural layer of pollen walls in angiosperms is usually columellate or granular. The columellate type, which consists of cylindrical columns supporting the tectum, is found generally associated with the semitectate (reticulate) or microperforate tectal condition (i.e., Trochodendrales, Hamamelidales, Daphniphyllales, Leitneriales, and Fagales). The granular infrastructure (loosely defined here), which can be composed of anastomosing rods, spherical granules, or irregular-shaped columns, is generally associated with taxa that have microchannels (i.e., Urticales, Juglandales, Myricales, and Casuarinales).

FOOTLAYER (ONE CHARACTER STATE)

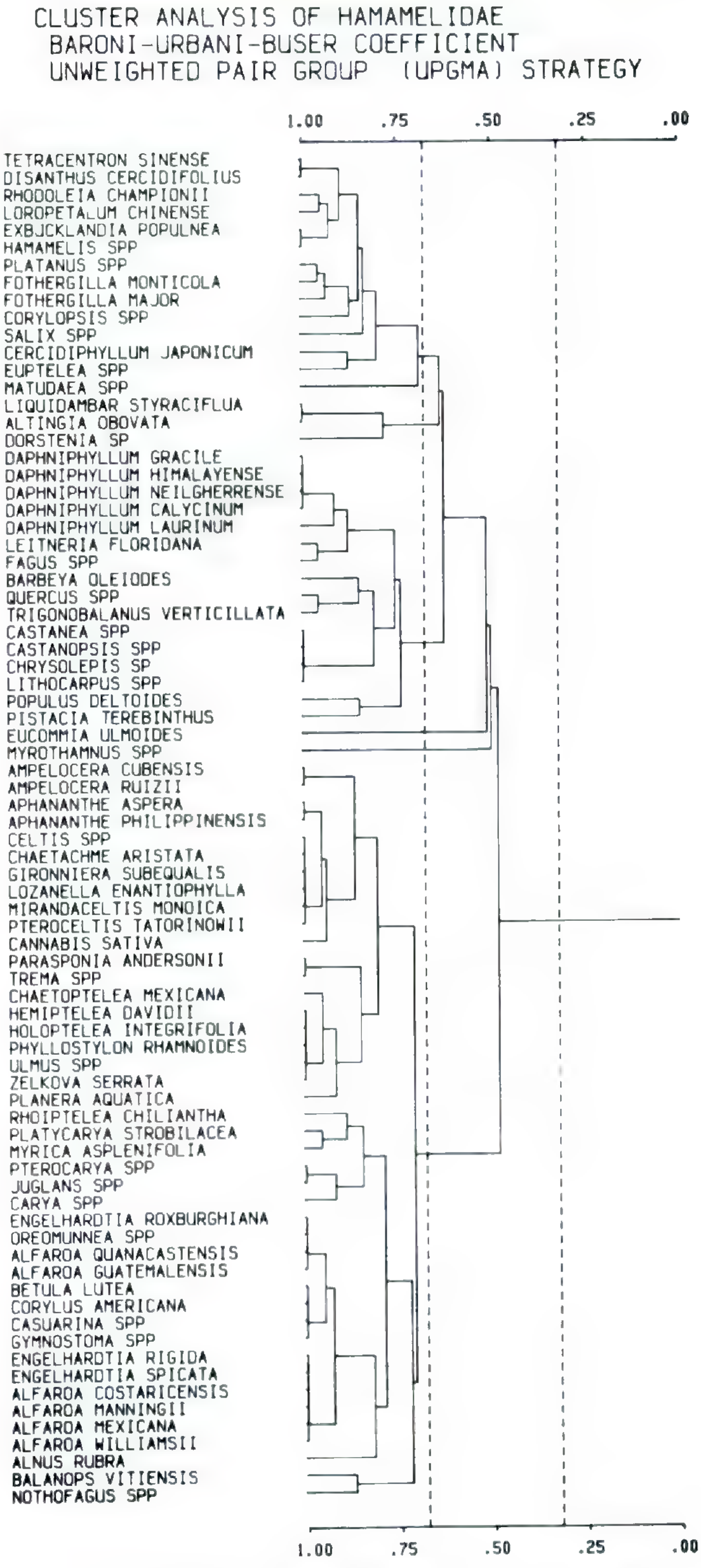
A footlayer is present in all taxa investigated except *Barbeya oleiodes,* in which it is represented by a very thin discontinuous layer, and much of the infrastructural layer rests directly on the endexine.

ENDEXINE (THREE CHARACTER STATES)

The presence, absence, and thickness in apertural and nonapertural regions of endexine varies among taxa. There appears to be no apparent relationship among taxonomic units and the occurrence of endexine. Three character states are recognized for this wall layer: (1) presence or absence, (2) endexine is thicker in the apertural regions than nonapertural regions, and (3) endexine does not thicken in the apertural region relative to nonapertural region. If endexine is absent, all three character states are scored (0). If endexine is present only in apertural region, character states one and three are (0) and two is (1) (this occurs only in *Rhodoleia*). If endexine is present but does not thicken in apertural region, character states one and three are (1) and two is (0).

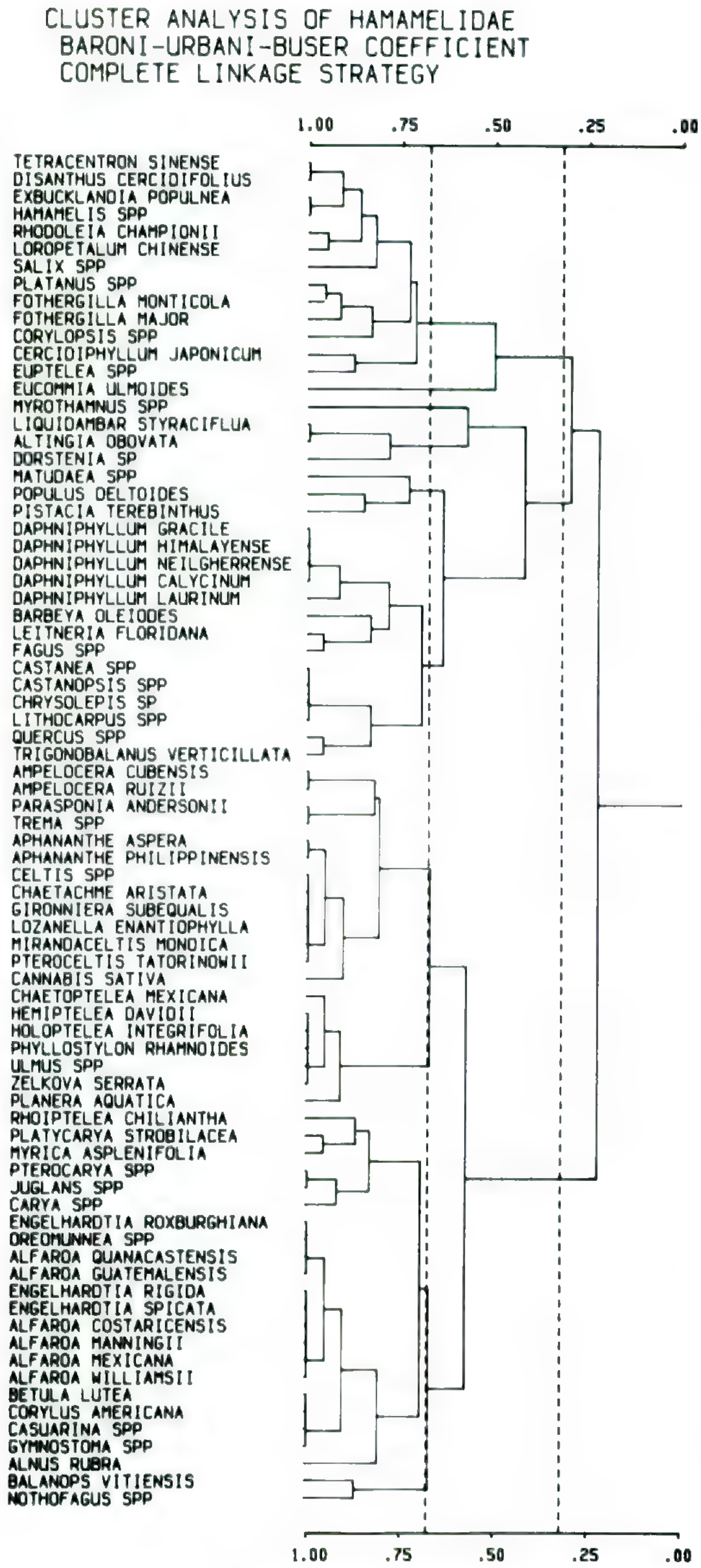
SIMILARITY CLUSTER ANALYSIS

The similarity cluster analysis used the Baroni-Urbani-Buser Coefficient. Using the Cluster Analysis Package of Archer, Hohn, and Horowitz (1984), two dendrograms were generated using the unweighted pair group method (UPGMA; Text-Fig. 1) and complete linkage strategies (CLS; Text-Fig. 2). Both produced similar results.



TEXT-FIGURE 1. Similarity cluster analysis, UPGMA strategy.

Three major groups are discernable, designated Group I, II, and III. Group I in both analyses consists of Trochodendraceae, Cercidiphyllaceae, Eupteleaceae, Platanaceae, Hamamelidaceae (including Liquidambaroideae), Eucommiaceae, and Myrothamnaceae. Group I taxa are prolate to spherical in equatorial view and circular in polar view. The tricolpate aperture pre-



TEXT-FIGURE 2. Similarity cluster analysis, CLS.

dominates; however, the pericolpate (*Euptelea, Matudaea*), periporate (Liquidambaroideae), and triporate (with ulceroid apertures, Myrothamnaceae) apertures are also present. Pollen is usually shed in monads (except in Myrothamnaceae). The tectum is usually reticulate, and the size of the perforations vary (except Eucommiaceae are atectate and Myrothamnaceae have clavate sculpturing). The infrastructure is predominantly columellate and all taxa have a footlayer. Endexine is usually present. Supratectal sculpturing is variable. In both linkage strategies, *Trochodendron* and *Tetracentron* exhibit close phenetic relationships with *Disanthus* of the Hamamelidaceae. The genera *Cercidiphyllum* and *Euptelea* also exhibit a high degree of similarity. Taxa of the Platanaceae and Hamamelidaceae (excluding the Liquidambaroideae) are also phenetically similar.

Some problematic taxa of Group I are the Liquidambaroideae, Eucommiaceae, and Myrothamnaceae. Members of these three groups occupy an intermediate position between Groups I and II, using the complete linkage strategy (Text-Fig. 2). However, using the unweighted pair group method, all three families appear isolated between groups II and III and may be considered groups themselves (Text-Fig. 1).

Group II is small and exhibits closer phenetic relationships with Group I than Group III. It consists of Daphniphyllaceae, Leitneriaceae, Barbeyaceae, and Fagaceae (excluding *Nothofagus*). Pollen is generally spherical but can be prolate or oblate in equatorial view and is tricolpate or tricolporate. Pollen is invariably shed in monads. The tectum is perforate, the perforations are usually not discernable with light microscopy but evident with SEM. The infrastructure of all taxa is columellate. The footlayer is present in all taxa except *Barbeya*. Endexine is occasionally present but best developed in *Barbeya*. Exine sculpturing is variable.

The clustering patterns of the taxa investigated in this group generally reflect familial relationships. The Daphniphyllaceae and Leitneriaceae are closely linked. Taxa of the Fagaceae form a group, except that *Fagus* exhibits a closer relationship with the Leitneriaceae and Daphniphyllaceae in both linkage strategies. The Barbeyaceae, although clearly members of this group, are somewhat isolated from the other taxa in both analyses.

Group III is the largest of the three groups, consisting of the Ulmaceae, Cannabaceae, Juglandaceae, Rhoipteleaceae, Betulaceae, Casuarinaceae, and Myricaceae, and the Balanopaceae and the genus *Nothofagus* as somewhat isolated entities. Pollen of this group is oblate in equatorial view and circular to angular in polar view. Aperture type consists of equatorially placed pores or short colpi, numbering two to many. Pollen is shed in monads. The tectum appears imperforate with SEM; however, TEM reveals that small channels traverse the tectum. Infrastructure varies somewhat but is generally granular to columellate-granular. The infrastructural layer

can consist of irregular-shaped rods, anastomosing rods, or spherical granules. The footlayer is usually thin, but always present. The endexine is relatively rare in this group and when present is usually a very thin layer and exine sculpturing can be rugulate, scabrate, or spinulose.

Branching patterns in this group generally reflect familial relationships. Using the unweighted pair group strategy (Text-Fig. 1), the Ulmaceae appear as three distinct groups: (1) members of the Celtidoideae, (2) *Trema* and *Parasponia,* and (3) Ulmoideae. Using the complete linkage strategy, two groups are evident: Ulmoideae and Celtidoideae (sensu Grudzinskaya, 1967). Cannabaceae link closely with the Celtidoideae in both strategies.

Juglandaceae (sensu Manning, 1978) are separated into four groups based on linkage patterns with the complete linkage strategy (Text-Fig. 2). *Platycarya* (Platycaryeae), isolated from other taxa of the Juglandaceae, exhibits similarities to *Rhoiptelea* and *Myrica. Pterocarya* and *Juglans* (Juglandeae) show close phenetic relationship with *Carya* (Hicoreae). Members of the Engelhardtieae comprise the fourth group closely linked with the Betulaceae and Casuarinaceae. The unweighted pair group strategy produced similar results, however, taxa of the Betulaceae and Casuarinaceae fall within the Engelhardtieae.

The Betulaceae and Casuarinaceae form a closely linked group in both strategies that is near or within the Engelhardtieae (Juglandaceae; Text-Figs. 1, 2).

Balanops and *Nothofagus* of the Fagaceae appear as a close group, isolated, but within Group III in both linkage strategies.

In addition to the taxa already discussed, four other taxa were introduced into the analysis: *Salix, Populus* (Salicaceae, Dillenidae), *Pistacia* (Rosideae), and *Dorstenia* (Moraceae).

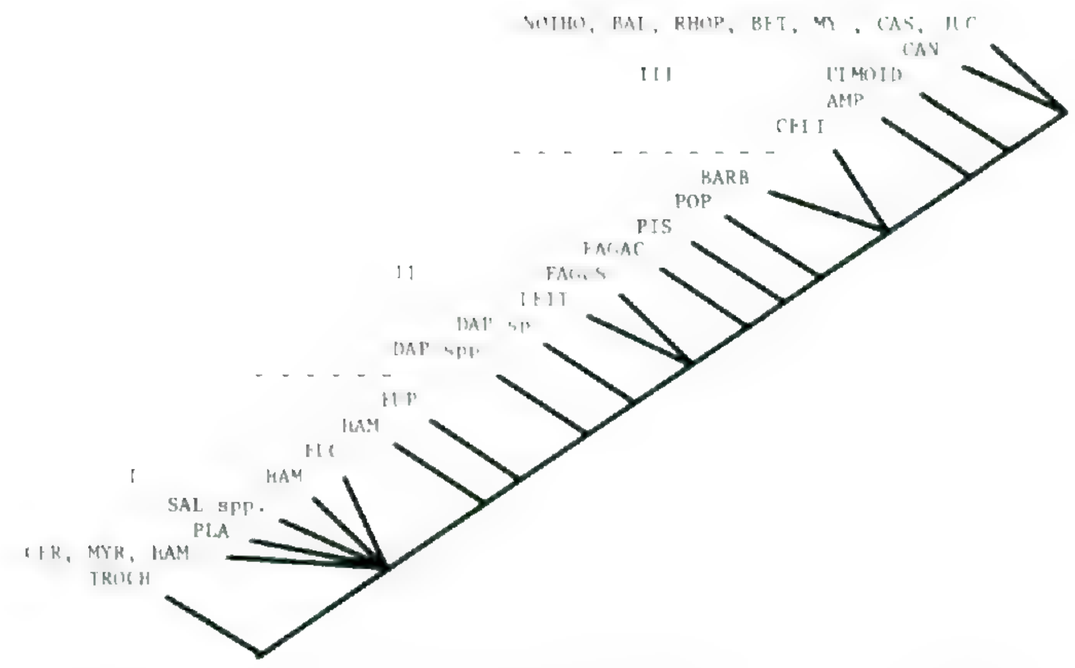
The Salicaceae were placed with amentiferous taxa, which are now members of the Hamamelidae by Engler (1926). *Salix* has tricolpate, spherical to prolate pollen, prolate, reticulate exine sculpturing, and a columellate infrastructure (Erdtman, 1952, 1969). Erdtman (1952) noted the similarity of *Salix* pollen to that of the Platanaceae. In our analysis, *Salix* is most similar to members of the Hamamelidaceae. *Populus* pollen is spherical and usually considered inaperturate; however, our TEM studies reveal a modification of the exine similar to pollen with ulcerate apertures (Fig. 72a). The tectum is perforate and the columellae rest on a very thin footlayer (Fig. 72b). With the complete linkage strategy *Populus* appears as an isolated taxon between Groups I and II (Text-Fig. 2), and between II and III in the unweighted pair group strategy (Text-Fig. 1). In both cases, neither *Salix* or *Populus* exhibits close phenetic relationships with amentiferous taxa of Group III. Pollen of *Pistacia* is 6–7-porate. The pores are distributed irregularly about the equator and are ulceroid in nature (Fig. 70). Pollen is spherical (Fig. 70) and shed in monads, and the tectum is perforate. The infrastructure is columellate; the columellae are fused to a relatively thick footlayer (Fig. 71), and no endexine is evident. Thorne (1973) considered the Juglandaceae and Rhoipteleaceae (Group III taxa, this study) to be closely allied with the Anacardiaceae (Rosideae). However, the pollen of *Pistacia* shows little phenetic relationship with that of the Juglandaceae or Rhoipteleaceae. *Pistacia,* along with the salicaceous taxa, form an isolated group between Groups I and II with the complete linkage strategy (Text-Fig. 2), and between II and III with the UPGMA strategy (Text-Fig. 1).

Pollen of *Dorstenia* (Moraceae), also included in the analysis, is periporate, spherical in shape, and its wall structure is tectate-granular with a well-developed footlayer (Fig. 73). The tectum is occasionally traversed by minute channels (Fig. 73). This taxon shows greatest phenetic similarity with members of the Liquidambaroideae (Hamamelidaceae) (Text-Figs. 1, 2). It is unlikely that the introduction into the analysis of a single taxon from such a large family as the Moraceae with about 1,000 species will accurately reflect familial relationships. Light and SEM studies of a few moraceous taxa (Niezgoda & Nowaczyk, 1976; Hamilton, 1976; Nair & Sharma, 1975; Zamora, 1977) indicate that the pollen is very diverse in the Moraceae, and a much broader survey is necessary before palynology can be used to suggest phenetic relationships with taxa of the Hamamelidae or any other subclass.

The Phylogenetic Analysis

The data set used for the similarity cluster analysis was also analyzed cladistically (Appendix II). The computer program used, Phylogenetic Analysis Uing Parsimony (PAUP), was developed and installed in the Indiana University computer system by David L. Swofford of the Illinois Natural History Survey (Swofford, 1984).

Seventy-eight operational taxonomic units



TEXT-FIGURE 3. Cladistic analysis of the Hamamelidae based on pollen (Adams, 1972, consensus tree). AMP = *Ampelocera*, BAL = Balanopaceae, BARB = Barbeyaceae, BET = Betulaceae, CAN = Cannabaceae, CAS = Casuarinaceae, CELT = Celtidoideae, CER = Cercidiphyllaceae, DAP = Daphniphyllaceae, EUC = Eucommiaceae, EUP = Eupteleaceae, FAGAC = Fagaceae, HAM = Hamamelidaceae, JUG = Juglandaceae, LEIT = Leitneriaceae, MY = Myricaceae, MYR = Myrothamnaceae, NOTHO = *Nothofagus*, PIS = *Pistacia*, PLA = Platanaceae, POP = *Populus*, RHOP = Rhoipteleaceae, SAL = *Salix*, TROCH = Trochodendrales, ULMOID = Ulmoideae.

(OTUs) and 30 pollen characters were analyzed. The character states are unordered; however, an outgroup was chosen. The consensus tree generated rooted the outgroup (Text-Fig. 3).

Tetracentron of the Trochodendrales was chosen as the outgroup for two reasons: (a) the Trochodendrales are considered by Cronquist (1981) and Endress (1986) to be the basal or the plesiomorphic group in the Hamamelidae, and (b) the pollen characters of the taxa in the Trochodendrales are common in many of the alleged primitive families and orders of other subclasses. The commonality of these characters suggests primitiveness (or the plesiomorphic state; see the descriptive palynology section for pollen characters).

From the consensus tree generated, three major phylogenetically related groups are evident. These groups are comparable to the groups recognized in the similarity cluster analysis (Text-Fig. 3; Groups I, II, and III). In addition to the consensus tree, the program generated 250 equally parsimonious trees. The branch swapping in all of the equally parsimonious trees takes place within these three groups, at all times maintaining the phylogenetic relationship of the three groups. Group I taxa always occur at the base of the tree, showing a close phylogenetic relationship with the outgroup. Group II taxa always occur as an intermediate group between I and III (Text-Fig. 3). Group III always occurs as the most derived. All groups exhibit a number of equally parsimonious possibilities within each group. This suggests that it is impossible to resolve the more specific phylogenetic relationships between members of each group based on pollen alone. Not surprisingly, in order to reach a finer resolution of the relationships at the generic or specific levels, characters other than pollen will have to be used.

The taxa from the Salicaceae and Anacardiaceae introduced into the analysis bear no phylogenetic relationship to the amentiferous taxa of Group III, again supporting the results of the similarity cluster analysis. *Salix* exhibits a close cladistic relationship to a member of the Hamamelidaceae, and *Populus* and *Pistacia* appear as paraphylletic groups between Group II and Group III taxa.

It can be concluded from this analysis that Group I taxa are primitive, Group II taxa are intermediate between I and III, and Group III taxa are derived.

DISCUSSION

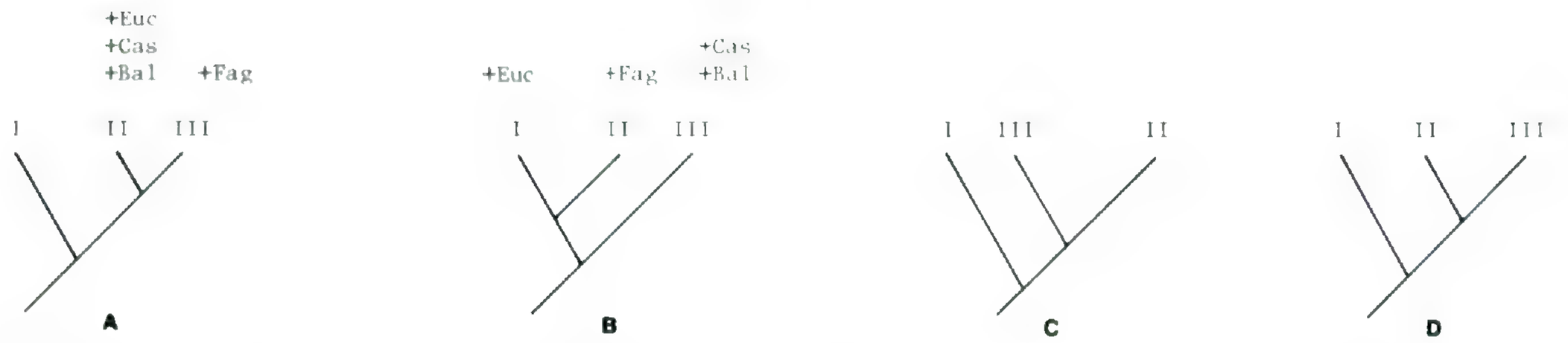
The taxonomic composition (at the family level) of the Hamamelidae has been a subject of controversy for some time. However, there is some agreement on the families that comprise the "core" taxa in this group. Both Thorne (1973) and Cronquist (1981) included the Trochodendraceae, Tetracentraceae, Cercidiphyllaceae, Eupteleaceae, Hamamelidaceae, and Platanaceae in the Hamamelidae (Hamamelidiflorae of Thorne, 1973). These families comprise a well-defined phenetic group based on vegetative (Group I of Barabe et al., 1982) and pollen characters (Group I, this study; Text-Figs. 1, 2). In addition, our cladistic analysis also suggests a close phylogenetic relationship among these taxa (Text-Fig. 3). The Eucommiaceae, a family Cronquist (1981) placed in its own order and Tippo (1938, 1940) considered closely related to the Urticales, are most similar to Group I taxa in our analysis. Based on a number of vegetative and floral characteristics, Thorne (1973) considered the Eucommiaceae closely allied with the Hamamelidales, as our analyses also suggest. The Myrothamnaceae are a problematic group. Based on pollen morphology, this family exhibits phenetic similarity to Group I taxa (also see Barabe et al., 1982) but has many unique pollen char-

acters not found in any other taxa in the Hamamelidae (also see Thorne, 1973). Cronquist (1981) placed this taxon in the Hamamelidales without question. Although our phenetic analysis does not show a strong relationship between *Myrothamnus* and other Group I taxa, our cladistic analysis demonstrates a close phylogenetic relationship between *Myrothamnus* and cercidiphyllaceous and hamamelidaceous taxa (Text-Fig. 3; cf. Cronquist, 1981).

Group II consists of a number of small, isolated families (Text-Figs. 1–3), which exhibit many pollen characters that can be considered intermediate between Groups I and III. Of the four families included in this group, Thorne (1973) considered only the Fagaceae as a member of the Hamamelidae. The Barbeyaceae (taxon incertae sedis of Thorne, 1973) are considered by Dickison and Sweitzer (1970) and Cronquist (1981) as closely allied with the Ulmaceae of the Urticales. However, Barabe et al. (1982) placed the family within their Group II (similar in composition to our Group II). On the other hand, our cladistic analysis clearly indicates a close relationship between *Barbeya* and the Celtidoideae of the Ulmaceae. The Daphniphyllaceae have been variously treated. Thorne (1973) considered this family allied with the Buxaceae and Brunelliaceae of the Rosidae. A recent cladistic analysis by Barabe (1984), using vegetative and floral features, lends support to Thorne's treatment. However, pollen data do not support this alliance; pollen of the Buxaceae is predominantly polyporate (Erdtman, 1952), and pollen of the Brunelliaceae, although tricolporate, is prolate with reticulate exine sculpturing (Cuatrecasas, 1970; similar to Group I pollen, this study). *Leitneria* (Leitneriaceae) is interesting because it has many features intermediate between Groups I and III. Its oblate shape and microperforate exine is characteristic of many Group III taxa and its tricolporate apertures are similar to some Group I taxa. In the compressed state (fossil pollen), it has a triradiate polar thickening (Fig. 53) that is reminiscent of some fossil normapollis types (e.g., some *Plicapollis*), a fossil group of dispersed pollen believed to be (in part) related to some Hamamelidae.

Group III taxa form the largest and closest knit phenetic group of the three. Results of the cladistic analysis show that the branching patterns among *Nothofagus, Balanops,* Rhoipteleaceae, Betulaceae, Myricaceae, Casuarinaceae, and Juglandaceae cannot be resolved based on pollen. The remaining taxa, all members of the Urticales, exhibit a high degree of paraphylesis (Text-Fig. 3). The phenetic and cladistic analyses based on pollen support Cronquist's (1981) treatment of these families. Thorne (1973) has argued for the placement of the Rhoipteleaceae, Juglandaceae, and Myricaceae in his Rutiflorae and suggested a close relationship of these families to the Anacardiaceae taxa. Our phenetic and cladistic analyses included the genus *Pistacia,* which Thorne believes to exhibit many characteristics suggestive of this alliance, a relationship our pollen data fails to support (Figs. 70, 71; Text-Figs. 1–3). The pollen characters that define Group III taxa (2–3 to many equatorially placed pores or short colpi, microchanneled tectum, columellate-granular infrastructure, thin footlayer, and thin endexine) represent a unique array of features in the dicots. The Poaceae with wind-pollinated porate pollen are the only family that show some convergence with Group III taxa, but this family has major differences in the placement and structure of the aperture; the annulate, distally located pores of pollen of the Poaceae are constructed by a thickening of the basal layer (Skvarla & Larson, 1966). The protruding pores in Group III taxa (aside from being equatorial apertures) are constructed by an elaboration of the tectum and infrastructure (Text-Fig. 7F–I). Thorne suggested that these taxa, as defined by Cronquist (1981), be separated into two different subclasses. Given the unique combination of characters in Group III, this suggestion finds little support in our analyses. The pollen data presented here lend support to Cronquist's system (1981). The following discussion of phylogenetic relationships of the Hamamelideae relies on the acceptance of these groups as monophyletic (sensu Cronquist, 1981).

The results of the phenetic and cladistic analyses are especially interesting when compared with the recent analysis by Barabe et al. (1982) and what is currently known about the fossil record of the Hamamelidae. The similarity cluster analysis of the Hamamelidae based on vegetative and floral characteristics by Barabe et al. (1982) distinguishes three groups. Group I consists of the same taxa that make up our Group I. Recall that Group I is made up of families that Thorne (1973) and Cronquist (1981) consider "core" taxa. The discrepancy between the analysis of Barabe et al. (1982) and our phenetic analysis concerns the relationship of Group II taxa to Groups I and III and the composition of Groups II and III.



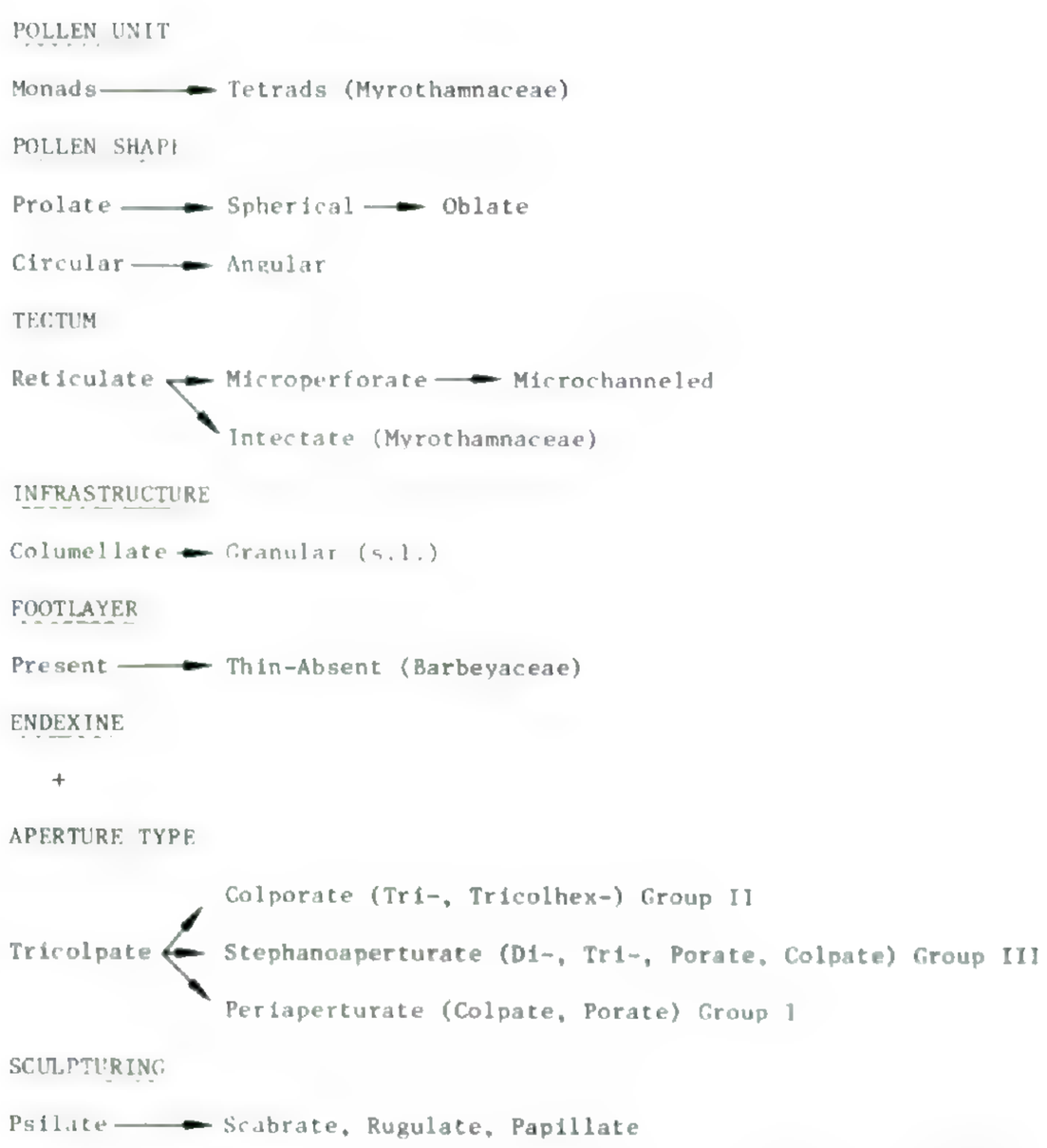
TEXT-FIGURE 4.—A. Phenetic relationships of the major groups recognized by Barabe et al. (1982). Except for the taxa listed above the groups, taxa within that group are the same as in our groups.—B. Phenetic relationships of the major groups determined in our analysis.—C. Phylogenetic relationships of the groups based on the fossil record.—D. Phylogenetic relationships of the major groups based on a cladistic analysis of the pollen characters and first occurrence of the pollen types represented by each group.

Group II of Barabe et al. (1982) consists of *Leitneria, Barbeya,* members of our Group II, Didymelaceae (not considered in our analysis), *Balanops* (a rather isolated member of our Group III), Casuarinaceae (member of our Group III), and Eucommiaceae (member of our Group I). However, in our study, *Eucommia* occurs as an isolated member between Groups I and II in the complete linkage strategy and between Groups II and III in the unweighted pair group strategy. Group III of Barabe et al. (1982) is very similar to our Group III except for their inclusion of the Fagaceae (Text-Fig. 4). The Fagaceae are members of our Group II. The general picture that emerges from their analysis is that Groups II and III are phenetically closer to each other than to Group I (Text-Fig. 4A). In our phenetic analysis of the pollen groups, I and II are closer to each other than either is to Group III (Text-Fig. 4B).

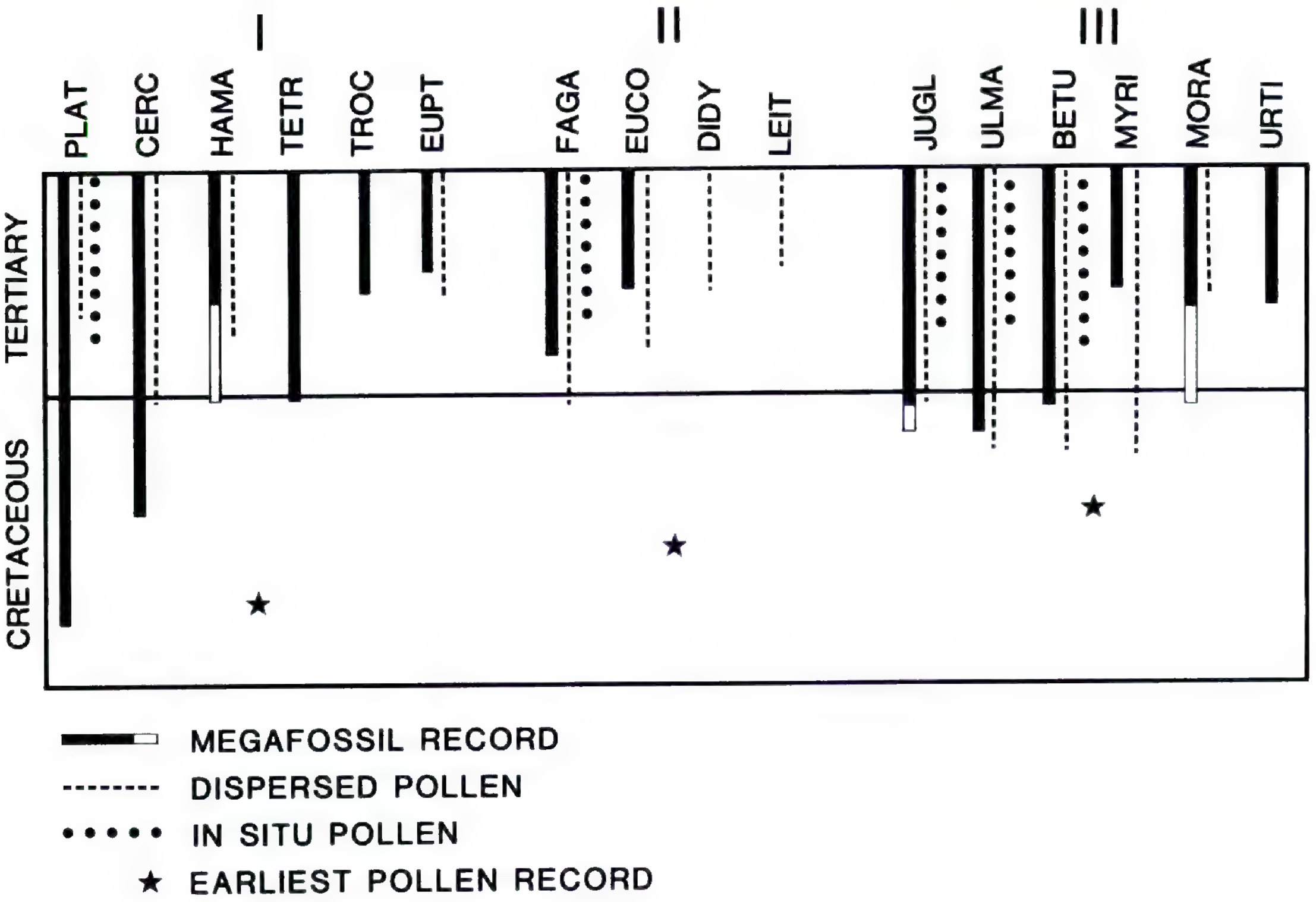
The relatively close agreement between the phenetic analysis of Barabe et al. (1982) and ours, especially in terms of the members of each group and the phenetic relationship between the three groups using different sets of characters, underscores the gradational nature of pollen, floral, and vegetative features among members of the three groups.

The results of the cladistic analysis compare well with the phenetic analyses of Barabe et al. (1982) and that presented in this study (Text-Fig. 4D). For the most part, the members of each phenetic group are maintained in the same relative position in the cladogram (Text-Fig. 4). The cladistic analyses indicate that Group I taxa are primitive. Group II taxa show features of Group I and III (and are intermediate between them), and Group III taxa are derived. However, the branching patterns within each of these groups are difficult if not impossible to resolve based on pollen data alone and will require an analysis that includes a wider range of characteristics than available in pollen.

The choice of *Tetracentron* (Trochodendrales) as our outgroup (see above), and the use of parsimony to derive the other taxa, orders the pollen characters (Text-Fig. 5). The pollen unit is predominantly a monad in all three groups. The occurrence of tetrads in the Myrothamnaceae is considered a derived condition. Pollen shape is primarily prolate in the primitive groups and oblate in the derived taxa. Likewise, shape in polar view ranges from circular in primitive taxa to angular in the derived groups. The tectum varies from reticulate in Group I to microperforate in Group II to microchanneled in Group III. Pollen wall structure is columellate in Groups



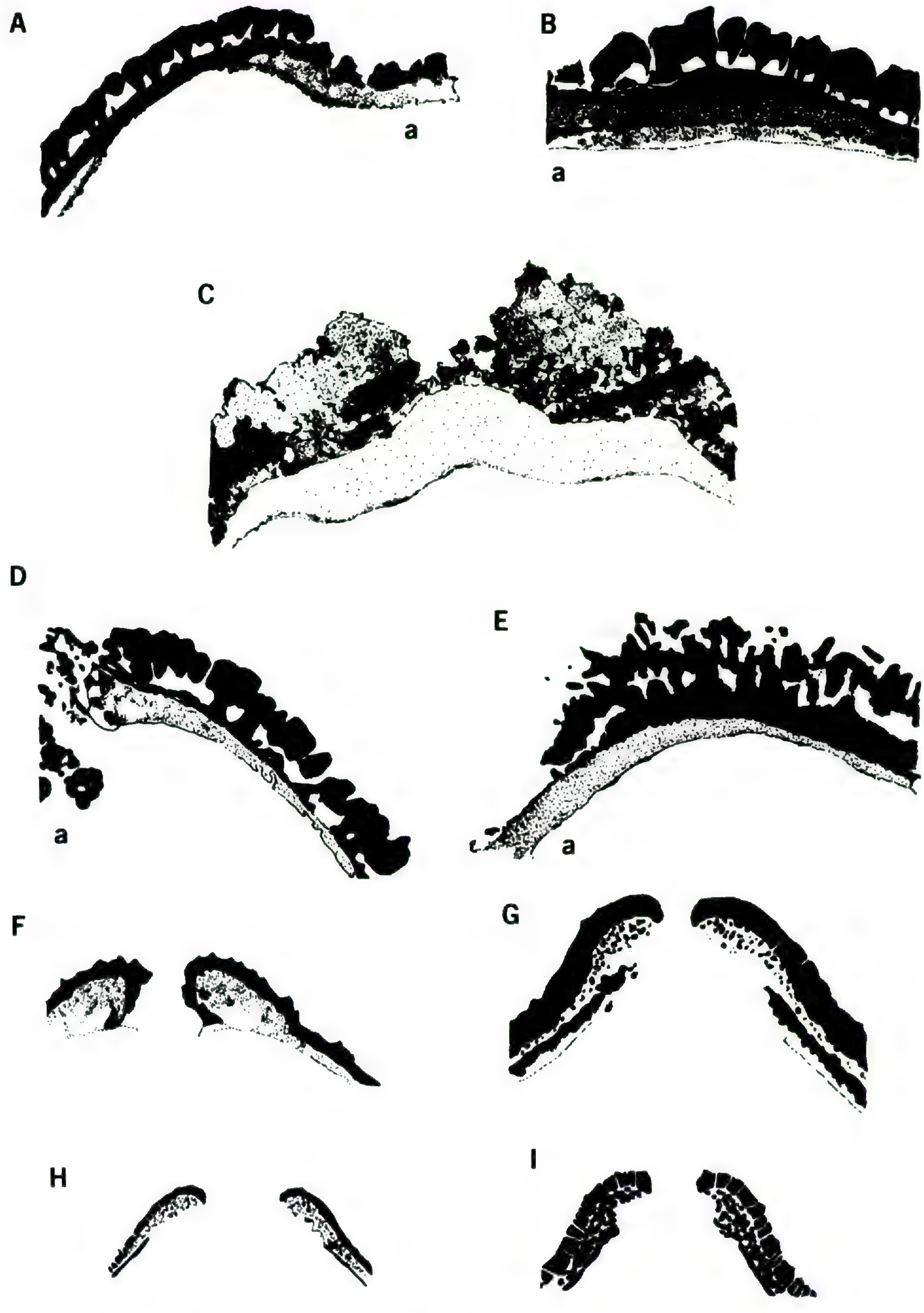
TEXT-FIGURE 5. Evolutionary trends of pollen characters in the Hamamelidae, based on a phenetic and cladistic analysis of extant pollen.



TEXT-FIGURE 6. The known fossil record of hamamelidaceous taxa. The earliest pollen record (*) is the earliest record of pollen similar to that found in the Hamamelidae group (not necessarily of hamamelid affinity). Compiled from Wolfe (1973), Manchester (1981), Jones (1984), Zavada and Crepet (1981), Upchurch (1984), and Crane (pers. comm.).

I and II (the plesiomorphic condition) and columellate to granular in Group III, with some taxa having an infrastructure composed of columellae-like elements and granules (e.g., *Balanops, Betula, Celtis*). The footlayer is present in all taxa except *Barbeya,* and this is considered a derived state. Pollen aperture type is predominantly tricolpate in Group I taxa and is considered the plesiomorphic condition. The periaperturate type may occur in Group I taxa (e.g., *Altingia*) but is considered a derived type in this group. Group II taxa are primarily tricolporate and Group III porate. Although it is convenient to consider Group II as an intermediate aperture type between I and III, it is just as likely that the porate type of Group III is derived directly from the tricolpate type. Thus, the aperture type of Group III can conceivably be derived from the Group II type (tricolporate) or Group I type (tricolpate). However, the most parsimonious transition is from the tricolpate type to porate condition because such a transition does not first require the evolution of the pore and then the reduction of the colpus, but only a reduction of the colpus. The polyporate pollen of the Liquidambaroideae (Group I) is also believed to be derived directly from the colpate condition based on its close phylogenetic relationship to the colpate pollen of some Hamamelidaceae.

The fossil record is also important in interpreting the neontological data. As indicated by the cladistic analysis, we might expect Group I taxa to appear first in the fossil record. The Platanaceae and Cercidiphyllaceae both appear before any of the other hamamelidaceous taxa, corroborating to some extent the neontological data (Text-Fig. 6). Group II taxa, however, appear as megafossils later than Group III taxa (Text-Fig. 6). This situation taken at face value supports our earlier suggestion that Group III taxa are as likely to be derived from Group I as Group II taxa. Thus, the order in which Groups II and III are derived would be reversed (Text-Fig. 3C). If the first occurrence in the fossil record of the pollen type for each of the three groups is considered, we find that Group I pollen appears first,



TEXT-FIGURE 7. A–E. Representative Group I and II taxa with endo-thickenings in the apertural region (redrawn) (a = aperture).—A. *Rhodoleia championii*; ×12,540.—B. *Leitneria floridana*; ×12,540.—C. *Barbeya oleoides*; ×8,094.—D. *Fagus crenata*; ×10,500 (redrawn from Crepet & Daghlian, 1980).—E. *Quercus spinosa*; ×13,250 (redrawn from Crepet & Daghlian, 1980). F–I. Representative Group III taxa with exo-thickenings in the apertural region.—F. *Cannabis sativa*; ×8,094.—G. *Rhoiptelea chiliantha*; ×13,500 (redrawn from Stone & Broome, 1971).—H. *Pterocarya delavayi*; ×3,700 (redrawn from Stone & Broome, 1975).—I. *Juglans mollisa*; ×8,200 (redrawn from Stone & Broome, 1975).

Group II shortly thereafter, and then Group III (Text-Fig. 6). However, unless these pollen types can be taxonomically related to the Hamamelidae, this cannot be construed as strong support for the intermediate position Group II seems to occupy based on the neontological data. However, the elucidation of the taxonomic affinities of many of the dispersed pollen taxa of the Normapollis group may have an influence on our interpretation of Hamamelid phylogeny. Many of these dispersed pollen types are believed to be related to amentiferous taxa (Kedves & Dinitz, 1981). Kedve's (1981, 1983) recent treatment of this fossil-dispersed pollen group is relevant; he recognized three major groups: probrevaxones, normapolles, and postnormapolles. Grains of the probrevaxones group are tricolporate with short colpi, have tectate-columellate wall, and reticulate to psilate to slightly verrucate-scabrate exine sculpturing. The germinal aperture lacks an annulus. Kedves (1981) subdivided the normapolles group into three subgroups: pronormapolles, eunormapolles, and paranormapolles. The pronormapolles are similar in many respects to the probrevaxones types except that they possess endannuli (a thickening in the inner part of the apertural region (e.g., *Complexiopollis, Limaipollenites*; Kedves & Pardutz, 1982). Members of the pronormapolles have, in addition to the tricolpate aperture, a microperforate exine and tectate columellate wall; shape is oblate in equatorial view and angular in polar view. The characters observed in both the probrevaxones and pronormapolles are similar to those in Groups I and II in our analysis. These pollen types are the stratigraphically earlier types and are considered the primitive types by Kedves (1983). The taxa of the subgroups eunormapolles and paranormapolles have many characteristics of our Group III taxa (columellate-granular infrastructure, thin basal layer, oblate equatorial shape, and circular to slightly angular shape in polar view; Stanley & Kedves, 1975; Kedves & Stanley, 1976). The presence of the annulate porate aperture is also common. In these fossil taxa the annulus is constructed of ektexinal material; this is also observed in the extant Group III taxa (Text-Fig. 7; compare Groups I and II taxa A–E with Group III taxa F–I). In addition to sharing many characteristics with Group III taxa, the Eunormapolles and paranormapolles taxa occur stratigraphically higher. Although the taxonomic affinities of the probrevaxones and pronormapolles groups are unknown, their chronistic relationship to the other normapolles—along with a suite of characters suggestive of Group II (or some Group I) taxa—makes it tempting to speculate that the probrevaxones and pronormapolles are hamamelidaceous taxa possibly related to some of the relictual Group II taxa of the extant Hamamelidae. However, elucidation of the taxonomic affinities of these dispersed pollen types will be much better understood when their attachment to megafossils is known. Until this is accomplished, the importance of this fossil material in determining the phylogenetic relationships of the Hamamelidae will remain speculative.

In summary, the phenetic and cladistic analyses based on pollen morphological data suggest the Hamamelidae as defined by Cronquist (1981) are a reasonably circumscribed subclass, and are in general agreement with other phenetic analyses (e.g., Barabe et al., 1982).

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APPENDIX I

Taxon	Collection	Locality	Herbarium
Altingia obovata Mers et Chun	*Liang 64734*	China	US
Balanops vitiensis (A. C. Smith) Hjedruqvist	*Degener 15519*	Fiji	US
Barbeya oleoides Schweinf.	*Burger 1926*	Ethiopia	US
Betula alba L.	*Knowlton*, 5/13/1933	Vermont	IU
Cannabis sativa L.	*Chase*, 8/23/1899	Illinois	IU
Casuarina stricta Ait.	*Christophel 3531*	Australia	—
Cercidiphyllum japonicum Sieb. et Zucc.	*Ya Tokuburchi s.n.*, 1891	Sapporo, Japan	US
Corylopsis pauciflora Sieb. et Zucc.	*Blaney 57613*	Japan (Cult.)	NYBG
Corylopsis willmottiae Rehol. et Wils.	*Rock 8127*	China	US
Daphniphyllum calycinum Benth.	*Chun 6428*	China	US
Daphniphyllum gracile Guff.	*Brass s.n.*	New Guinea	US
Daphniphyllum himalayense var. *chartaceum* (Rozenth.) Uuang	*Datla s.n.*	Siwalik	US
Daphniphyllum laurinum (Benth.) Bail.	*Boeea 7381*	Sumatra	US
Daphniphyllum neilgherrense (Wight) Thw.	*Bernardi 15811*	Ceylon	US
Disanthus cercidifolius Maxim.	*Maelsawa 409*	Japan	US
Dorstenia sp.	Coll. Ig. nom. *s.n.*	Connecticut (Cult.)	CONN
Eucommia ulmoides Oliv.	Coll. Ig. nom., 4/27/1932	Brooklyn Botanical Garden	BKL
Euptelea polyandra Sieb. et Zucc.	*Kobayashi & Oonisi 34579*	Japan	US
Exbucklandia populnea (R. Br. ex Griff.) R. W. Brown	*Rock 7574*	China	US
Fothergillia major Lodd.	*Hurbison 5930*	Georgia	US
Fothergillia monticola Ashe	*Walker 9816*	Pennsylvania	US
Gymnostoma deplancheanum (Miq) L.J.	*Christophel 3488*	New Caledonia	—
Hamamelis japonica Sieb. et Zucc.	*Konta 4923*	Japan	US
Hamamelis vernalis Sarg.	*Sally 1018*	Arkansas	US
Hamamelis virginiana L.	*Fosberg 45888*	Virginia	US
Leitneria floridana Chapm.	*Demaree 31693*	—	IU
Liquidambar styraciflua L.	*Burbank 2012*	Georgia	US
Lorapetalum chinense Oliv.	*Tsung 23400*	China	US
Matudaea hirsuta Lundell	*Bogle 848*	Mexico	US

APPENDIX I. Continued.

Taxon	Collection	Locality	Herbarium
Myrica asplenifolia L.	*Deam 27402*	Indiana	IU
Myrothamnus flabellifolia Welw.	*Bayliss* BS/1762	Swaziland	US
Myrothamnus moschatus Bail.	*Fosberg 52576*	Madagascar	US
Pistacia terebinthus L.	*Young 9105*	Italy	IU
Platanus gentryi Nixon et Poole	*Gentry 5862*	Sinaloa, Mexico	MICH
Platanus kerrii Gagnep.	*Langson 8745*	Vietnam	—
Platanus mexicana Moric.	*Ventura 596*	Veracruz, Mexico	ENCB
Platanus mexicana Moric.	*Vela,* 2/22/1962	Puebla, Mexico	ENCB
Platanus occidentalis L. var. *occidentalis*	*Poole & Watson 2522*	Texas	TEX
Platanus racemosa Nutt.	*Ferris 8505*	Baja, California, Mexico	DS
Platanus racemosa Nutt.	*Elmer 3831*	California	NY
Platanus rzedowski Nixon et Poole	*King 3900*	San Luis Potosí, Mexico	MICH
Platanus wrightii Wats.	*Frye & Frye 2271*	Sonora, Mexico	DS
Platanus wrightii Wats.	*McVaugh 8105*	Hidalgo, Mexico	MICH
Populus deltoides Marsh	*Welch 5436*	Indiana	IU
Rhodoleia championii Hook. F.	*Hu,* 1/14/1972	Hong Kong	US

APPENDIX II

Appendix II lists the presence (1) or absence (0) of the 30 character states for each of the 78 taxa (OTUs). The * indicates the outgroup used in the cladistic analysis.

1	Tricolpate	TET SIN	*Tetracentron sinense*	HEM DAV	*Hemiptelea davidii*
2	Periporate	CER JAP	*Cercidiphyllum japonicum*	HOL INT	*Holoptelea integrifolia*
3	Pericolpate			PHY RHA	*Phyllostylon rhamnoides*
4	Triporate	EUP SPP	*Euptelea* spp.		
5	Atectate	PLA SPP	*Platanus* spp.	PLA AQU	*Planera aquatica*
6	Stephanocolpate	MYR SPP	*Myrothamnus* spp.	ULM SPP	*Ulmus* spp.
7	Tricolporate	LIQ STY	*Liquidambar styraciflua*	ZEL SER	*Zelkova serrata*
8	Stephanoporate	ALT OBO	*Altingia obovata*	CAN SAT	*Cannabis sativa*
9	Diporate	RHO CHA	*Rhodoleia championii*	DOR SP	*Dorstenia* sp.
10	Monads	EXB POP	*Exbucklandia populnea*	LEI FLO	*Leitneria floridana*
11	Tetrads	DIS CER	*Disanthus cercidifolius*	RHO CHI	*Rhoiptelea chiliantha*
12	Prolate	HAM SPP	*Hamamelis* spp.	PLA STR	*Platycarya strobilacea*
13	Spherical	LOR CHI	*Loropetalum chinense*	ENG ROX	*Engelhardtia roxburghiana*
14	Oblate	COR SPP	*Corylopsis* spp.		
15	Intectate	FOT MAJ	*Fothergilla major*	ENG RIG	*Engelhardtia rigida*
16	Semitectate	FOT MON	*Fothergilla monticola*	ENG SPI	*Engelhardtia spicata*
17	Microperforate	MAT SPP	*Matudaea* spp.	ORE SPP	*Oreomunnea* spp.
18	Microchannels	DAP GRA	*Daphniphyllum gracile*	ALF COS	*Alfaroa costaricensis*
19	Columellate	DAP LAU	*Daphniphyllum laurinum*	ALF QUA	*Alfaroa quanacastensis*
20	Granular	DAP HIM	*Daphniphyllum himalayense*	ALF GUA	*Alfaroa guatamalensis*
21	Footlayer			ALF MAN	*Alfaroa mexicana*
22	Endexine	DAP NEI	*Daphniphyllum neilgherrense*	ALF WIL	*Alfaroa manningii*
23	Endexine thickened in apertural region	DAP CAL	*Daphniphyllum calycinum*	ALF WIL	*Alfaroa williamsii*
				PTE SPP	*Pterocarya* spp.
				JUG SPP	*Juglans* spp.
24	Endexine not thickened in apertural region	EUC ULM	*Eucommia ulmoides*	CAR SPP	*Carya* spp.
		BAR OLE	*Barbeya oleiodes*	MYR ASP	*Myrica asplenifolia*
		AMP CUB	*Ampelocera cubensis*	BAL VIT	*Balanops vitiensis*
		AMP RUI	*Ampelocera ruizii*	CSN SPP	*Castanea* spp.
25	Psilate	APH ASP	*Aphananthe aspera*	CAT SPP	*Castanopsis* spp.
26	Scabrate	APH PHI	*Aphananthe philippinensis*	CHR SP	*Chrysolepis* sp.
27	Rugulate-verrucate	CEL SPP	*Celtis* spp.	LIT SPP	*Lithocarpus* spp.
				FAG SPP	*Fagus* spp.
28	Spinulose	CHA ARI	*Chaetachme aristata*	NOT SPP	*Nothofagus* spp.
29	Clavate	GIR SUB	*Gironniera subequalis*	QUE SPP	*Quercus* spp.
30	Striate	LOZ ENA	*Lozanella enantiophylla*	TRI VER	*Trigonobalanus verticillata*
		MIR MON	*Mirandaceltis monoica*		
		PTE TAT	*Pteroceltis tatorinowii*	ALN RUB	*Alnus rubra*
		PAR AND	*Parasponia andersonii*	BET LUT	*Betula lutea*
		TRE SPP	*Trema* spp.	COR AME	*Corylus americana*
		CHA MEX	*Chaetoptelea mexicana*	CAS SPP	*Casuarina* spp.
				GYM SPP	*Gymnostoma* spp.
				POP DEL	*Populus deltoides*
				PIS JER	*Pistacia terebinthus*
				SAL SPP	*Salix* spp.

APPENDIX II. Continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
TET SIN*	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	1	1	1	0	1	0	0	0	0	0
CER JAP	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	1	1	0	1	0	1	0	0	0	0
EUP SPP	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0	0
PLA SPP	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	1	1	0	1	1	0	0	0	0	0
MYR SPP	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0
LIQ STY	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0
ALT OBO	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0
RHO CHA	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0
EXB POP	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0
DIS CER	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	1	1	1	0	1	0	0	0	0	0
HAM SPP	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0
LOR CHI	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0
COR SPP	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	0	1	1	0	1	1	0	0	0	0	0
FOT MAJ	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	1	1	0	0	0	0	0
FOT MON	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	1	1	0	0	0	0	0
MAT SPP	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	1	0	1	1	0	0	0	0	0
DAP GRA	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	1	1	0	0	0	1	0	0	0
DAP LAU	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	1	1	0	1	0	0	0	0	0
DAP HIM	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	1	1	0	0	0	1	0	0	0
DAP NEI	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	1	1	0	0	0	1	0	0	0
DAP CAL	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	1	1	1	0	0	0	1	0	0	0
EUC ULM	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0
BAR OLE	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	1	0	0	1	1	0	0	1	0	0	0	0
AMP CUB	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
AMP RUI	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
APH ASP	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
APH PHI	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
CEL SPP	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
CHA ARI	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
GIR SUB	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
LOZ ENA	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
MIR MON	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
PTE TAT	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
PAR AND	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0
TRE SPP	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0
CHA MEX	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0
HEM DAV	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0
HOL INT	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0
PHY RHA	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0
PLA AQU	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0
ULM SPP	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0
ZEL SER	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0
CAN SAT	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
DOR SP	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1	0	0	0
LEI FLO	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	1	0	1	1	1	0	0	0	1	0	0	0
RHO CHI	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	0	1	0	0	0	1	0	0
PLA STR	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	1	0	1	0	0	0	1	0	0
ENG ROX	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
ENG RIG	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
ENG SFI	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
ORE SPP	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
ALF COS	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
ALF QUA	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
ALF GUA	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
ALF MAN	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
ALF MEX	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
ALF WIL	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
PTE SPP	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	1	0	1	0	0	0	1	0	0
JUG SPP	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	1	0	1	0	0	0	1	0	0
CAR SPP	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	1	0	1	0	0	0	1	0	0
MYR ASP	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	0	1	0	0	0	1	0	0
BAL VIT	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0
CSN SPP	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	1
CAT SPP	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	1
CHR SP	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	1
LIT SPP	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	1
FAG SPP	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	1	0	1	1	1	0	0	0	1	0	0	1
NOT SPP	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0
QUE SPP	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	0	0	1	1	0	0	0
TRI VER	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1	0	0	1	0	0	0	0
ALN RUB	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	1	1	0	0
BET LUT	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1
COR AME	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1
CAS SPP	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1
GYM SPP	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1
POP DEL	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	0	0
PIS JER	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	1	1	1	0	0	1	0	0	0	0
SAL SPP	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0

MORPHOLOGY AND DEVELOPMENT OF PISTILLATE INFLORESCENCES IN EXTANT AND FOSSIL CERCIDIPHYLLACEAE[1]

PETER R. CRANE[2] AND RUTH A. STOCKEY[3]

ABSTRACT

Comparison of the shoots, pistillate inflorescences, and infructescences of *Joffrea speirsii* Crane & Stockey from the upper Paleocene of Canada, *Nyssidium arcticum* (Heer) Iljinskaya from the upper Paleocene of southern England, and *Trochodendrocarpus arcticus* (Heer) Kryshtofovich from the lower Paleocene of Amur, eastern U.S.S.R., reveals considerable diversity in phyllotaxy, shoot growth, inflorescence position, and the number and crowding of follicles in each infructescence. Despite this diversity, the pistillate inflorescences of all these fossil *Cercidiphyllum*-like plants are directly comparable in basic organization, to inflorescences of extant *Cercidiphyllum*. These similarities add to the evidence that the fossil and extant taxa are closely related and support the view that the condensed inflorescence of *Cercidiphyllum* evolved by reduction from an elongated form. In extant *Cercidiphyllum* each flower consists of a single carpel, but in fossil taxa flowers may contain either one or two carpels. The arrangement of carpels in bicarpellate flowers resembles that in extant Hamamelidaceae.

The Cercidiphyllaceae contain a single genus, *Cercidiphyllum*, with two very similar species of dioecious trees, *C. japonicum* Siebold & Zuccarini native to Japan and central and western China, and *C. magnificum* (Nakai) Nakai native to Honshu (Spongberg, 1979). The Cercidiphyllaceae have been placed in the Hamamelidales (Cronquist, 1981) or treated as a separate order, Cercidiphyllales, within the Hamamelidae (Takhtajan, 1969). *Cercidiphyllum* is thought to be "related on the one hand to the Hamamelidaceae (especially *Disanthus*) and on the other to the Trochodendrales and Magnoliales" (Cronquist, 1981: 167), although most authors agree that *Cercidiphyllum* is an isolated genus separated by large morphological gaps from its closest living relatives. The pistillate reproductive structures of *Cercidiphyllum* are unusual: they superficially resemble an apocarpous flower with two to eight carpels, but the carpel orientation is apparently anomalous, with the ventral suture directed abaxially. Swamy and Bailey (1949) supported the earlier hypotheses of Brown (1939), Harms (1916), and Solereder (1899), and interpreted the pistillate reproductive structure as a reduced inflorescence. As part of the evidence for this hypothesis Brown (1939) and Swamy and Bailey (1949) cited the elongated inflorescences of fossil *Cercidiphyllum*-like plants, which were widespread at middle and high latitudes of the Northern Hemisphere during the Upper Cretaceous and lower Tertiary (Brown, 1939, 1962; Chandrasekharam, 1974; Schloemer-Jäger, 1958). Although this hypothesis has been discussed by subsequent authors, the precise similarities between the fossil and extant inflorescences have remained obscure due to inadequate understanding of the fossil material. In recent years knowledge of these fossil plants has increased considerably (Crane, 1984; Crane & Stockey, 1985; Krassilov, 1976; Stockey & Crane, 1983). They are now known from seedlings, leaves, shoots, pistillate inflorescences, infructescences, seeds, and possible staminate inflorescences, and it is clear that these extinct *Cercidiphyllum*-like plants are more closely related to *Cercidiphyllum* than to any other genus (Crane & Stockey, 1985). In this paper we compare the

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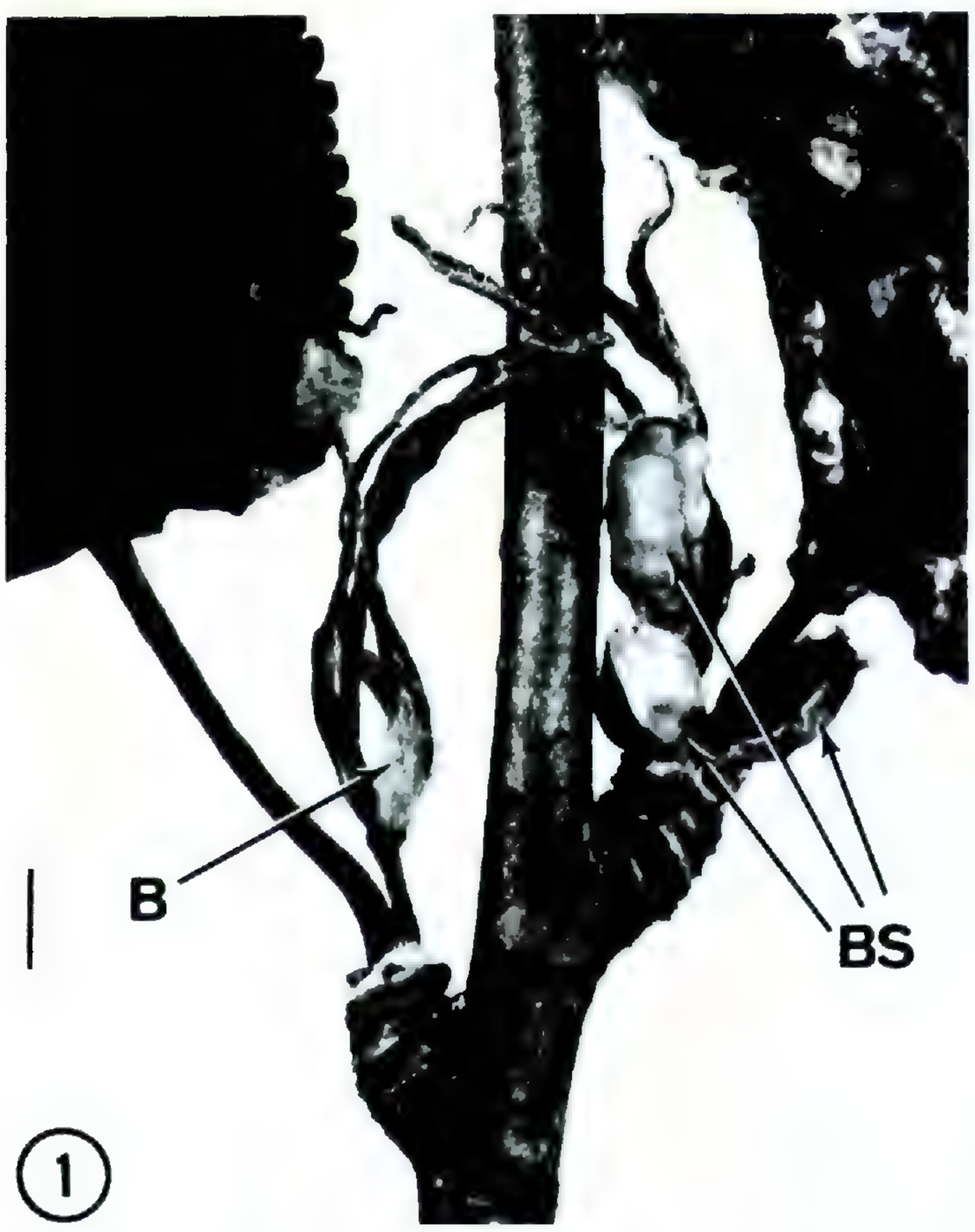

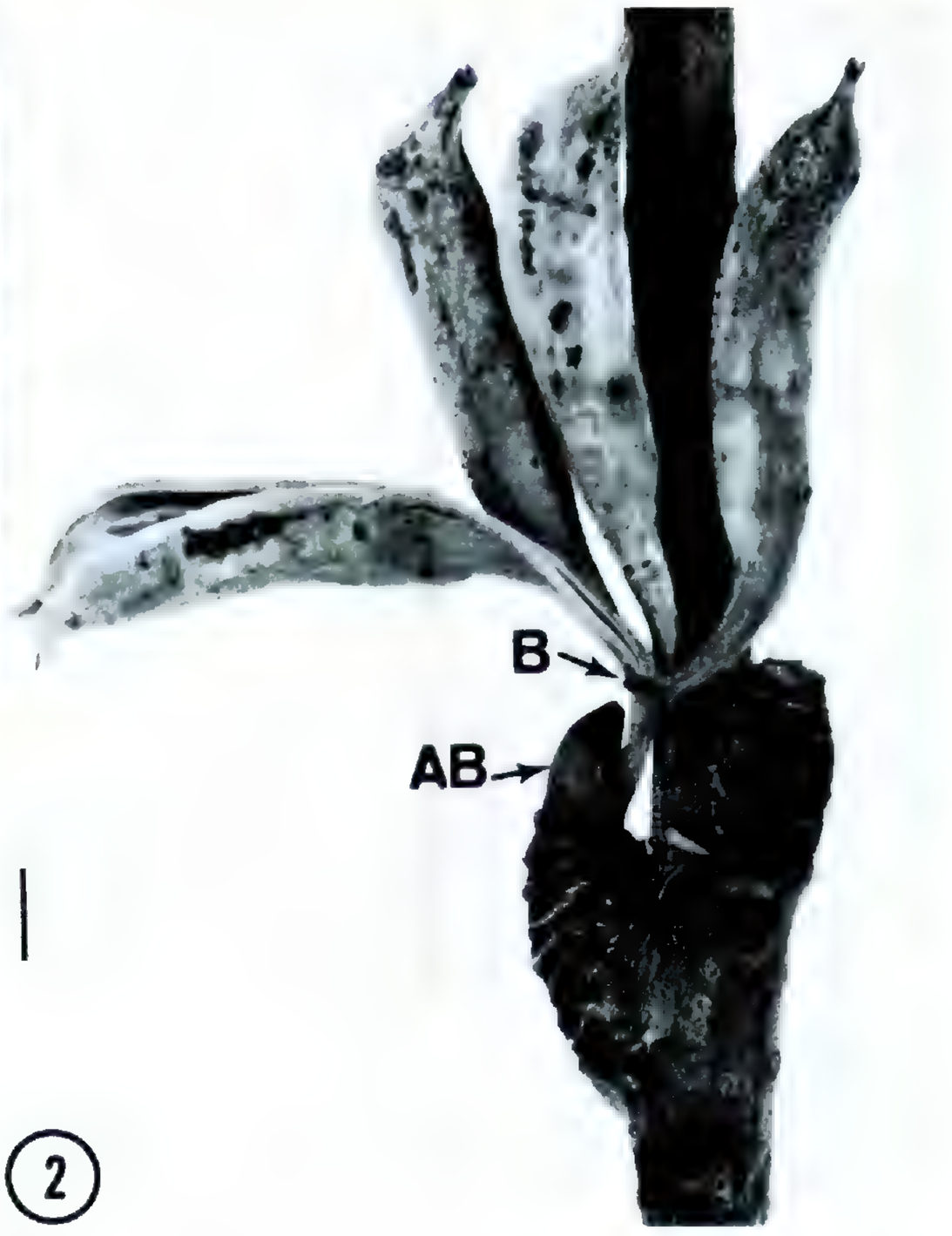

FIGURES 1, 2. *Cercidiphyllum japonicum* Sieb. & Zucc.—1. Two short shoots with young pistillate inflorescences and leaves: note the long styles and stigmas, and three bud-scales (BS) surrounding the inflorescence and leaf on the right: inflorescence on left shows a bract (B) subtending one of the four carpels, ×3.5.—2. Two curved short shoots showing leaf scars, axillary bud (AB), infructescence with four follicles, and bract scars (B) at base of follicles, ×3.3. Scale bars, 2 mm.

shoots and pistillate reproductive structures of extant *Cercidiphyllum* with early Tertiary *Cercidiphyllum*-like plants from western Canada (*Joffrea speirsii* Crane & Stockey, 1985), southern England [*Nyssidium arcticum* (Heer) Iljinskaya; Crane, 1984], and eastern U.S.S.R. [*Trochodendrocarpus arcticus* (Heer) Kryshtofovich; Krassilov, 1973, 1976]. The nomenclature for fossil taxa follows that adopted in Crane (1984), Crane and Stockey (1985), and Krassilov (1976). Discussion of the complex nomenclature and systematics of fossil *Cercidiphyllum*-like infructescences is outside the scope of this paper. Comparisons among fossil taxa demonstrate considerable diversity in phyllotaxy, shoot growth, inflorescence position, and the number and crowding of follicles in each infructescence. However, there are fundamental similarities in construction of the pistillate reproductive structures in the extant and fossil plants. These similarities add to the evidence that the fossil and extant taxa are closely related, explain some of the unusual morphological features of extant *Cercidiphyllum,* and facilitate more meaningful comparison of the genus with other extant taxa in the Hamamelidae.

EXTANT *CERCIDIPHYLLUM*

Extant *Cercidiphyllum* has branches differentiated into long and short shoots. In trees that we have examined, long shoot leaves are opposite, subopposite, or occasionally in irregular whorls of three. Short shoots develop from the axillary buds of long shoot leaves. Each axillary bud has three bud-scales (Figs. 1, 19); the outer and inner are positioned opposite to the second bud-scale and the leaf of the preceding season. The new leaf develops opposite the inner bud-scale (Swamy & Bailey, 1949), and each short shoot bears a single leaf in each growing season (Fig. 1). Short shoot growth is sympodial, continuing each season through the activity of a new axillary bud. The resulting short shoots are distinctly curved toward the long shoot on which they are borne (Fig. 2).

In fertile short shoots the pistillate inflorescence is terminal and consists of a short axis that has a cluster of two to eight carpels at the apex

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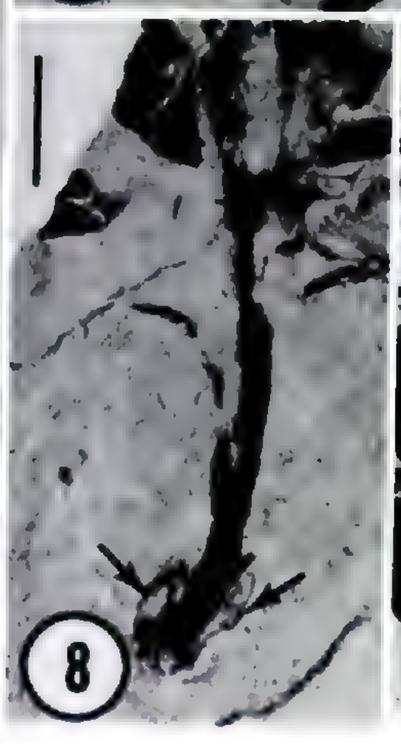
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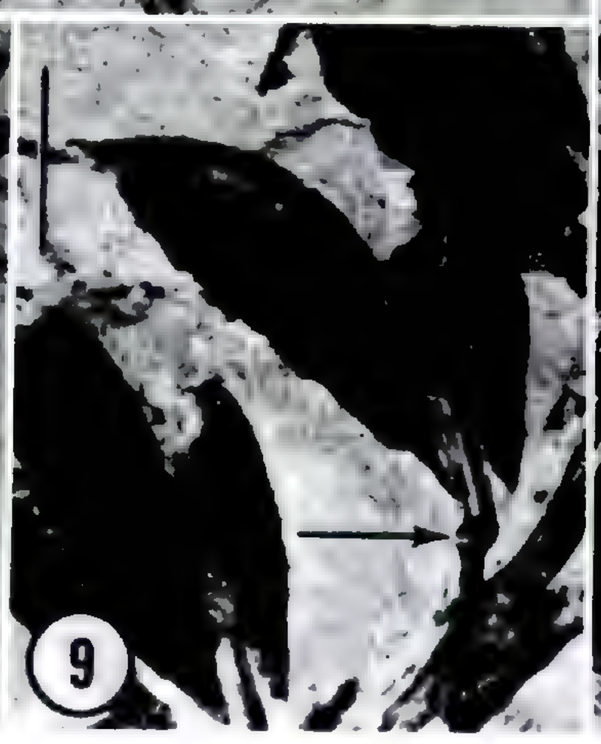
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(Figs. 1, 2). The carpels are arranged in opposite and decussate pairs, and the pairs are borne at slightly different levels (Swamy & Bailey, 1949). Each carpel is subtended by a membranous bract (Fig. 1) that is shed early in carpel development, leaving only a scar and sometimes a small flap of tissue at the base of the mature follicle (Fig. 2). The mature infructescence, including follicles, is up to 25 mm long. Attachment of pairs of carpels at different levels and the single bract associated with each carpel (Swamy & Bailey, 1949) are not consistent with the suggestion that the cluster of carpels is a simple apocarpous flower (Hutchinson, 1964). Each bract and the single carpel that it subtends are more readily interpreted as a single flower that lacks a perianth. The cluster of carpels is therefore an inflorescence of two to eight very simple flowers (Endress, 1986; Swamy & Bailey, 1949). The ventral suture of each carpel is oriented abaxially with respect to the inflorescence axis.

JOFFREA SPEIRSII CRANE & STOCKEY (PALEOCENE, CANADA)

Joffrea speirsii Crane & Stockey, from the upper Paleocene, Paskapoo Formation of central Alberta, Canada (Crane & Stockey, 1985), is the most completely understood of all fossil *Cercidiphyllum*-like plants. *Joffrea* exhibits long and short shoot differentiation. Although the short shoots are often alternately arranged, leaf scars on the short shoots (Fig. 5) indicate that the leaves were borne in opposite and decussate pairs; an arrangement also clearly seen in the seedlings of *Joffrea* (Crane & Stockey, 1985; Stockey & Crane, 1983). The number of leaves borne on each short shoot in a single growing season is unknown. In *Joffrea* at least some short shoots bore two or more pistillate inflorescences at the apex (Fig. 3). Neither this nor the short shoot leaf arrangement can be accounted for by sympodial growth. Together these features strongly suggest that short shoot growth was monopodial, with pistillate inflorescences developing from axillary buds of short shoot leaves.

The pistillate inflorescence is elongated, up to 65 mm long, with bud-scales at the base (Figs. 3, 8). The inflorescence bears approximately 40 carpels spaced at intervals of 1–5 mm on short side branches of the inflorescence axis (Fig. 3). Each side branch bears one or two short-stalked carpels. The junction between the carpel stalk and the side branch of the inflorescence axis is marked by a distinct joint (Fig. 9), which may mark the attachment of a caducous bract as in extant *Cercidiphyllum*. Single carpels or pairs of carpels frequently have broken away from the inflorescence axis at this joint (Fig. 7). At maturity, the inflorescence elongated to approximately twice its original length, and the follicles were more widely spaced at intervals of 6–11 mm (Fig. 4). At this stage the joint at the base of the follicles is often difficult to detect; however, well-preserved impressions of similar (perhaps conspecific) infructescences from the upper Paleocene of Montana clearly illustrate this joint and the tendency of the follicles to break away at that point (Figs. 13, 15). *Joffrea* carpels that are borne singly have the ventral suture oriented adaxially with respect to the inflorescence axis, and carpels borne in pairs have the two sutures opposite each other (Figs. 6, 7). At maturity at least some of the single follicles twisted so that the ventral suture was oriented abaxially with respect to the inflorescence axis (Fig. 10).

NYSSIDIUM ARCTICUM (HEER) ILJINSKAYA (PALEOCENE, ENGLAND)

Cercidiphyllum-like infructescences and follicles from the upper Paleocene Reading Beds

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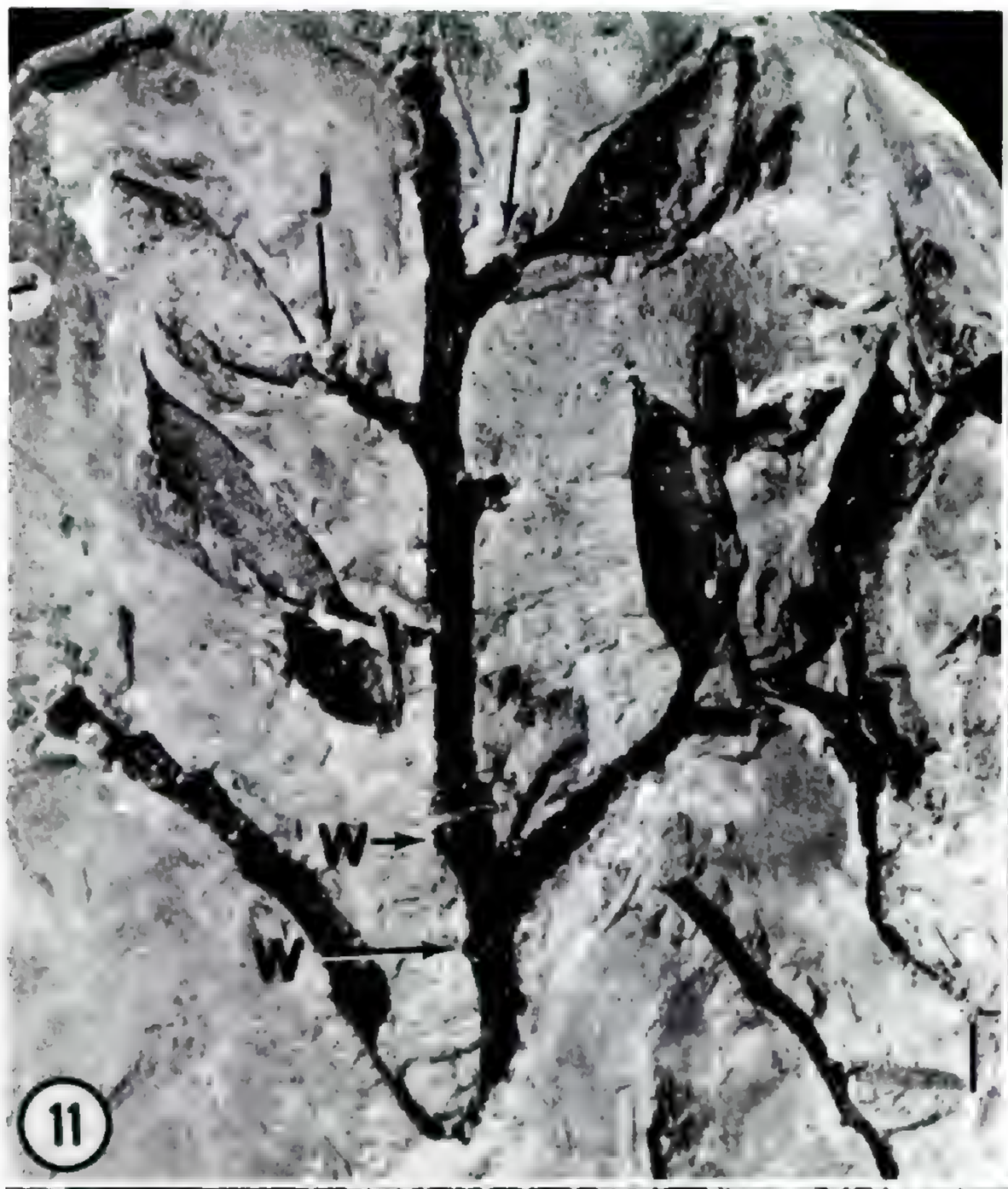
FIGURES 3–10. *Joffrea speirsii* Crane & Stockey, from Red Deer, Alberta (Paskapoo Formation, upper Paleocene). All specimens (prefix S) in the University of Alberta Paleobotanical Collections (UAPC-ALTA).—3. Long shoot with attached short shoots: lower short shoot showing two attached pistillate inflorescences, a bud-scale (arrow), and an incomplete third axis or petiole (S11437A), ×1.6.—4. Mature infructescence showing widely spaced follicles borne both singly and in pairs (S13357A), ×0.95.—5. Short shoot showing diamond-shaped leaf scars: an opposite pair indicated with arrows (S13333), ×3.7.—6. Ridged infructescence axis from which a pair of follicles have abscissed: note sutures facing one another (S12358), ×1.75.—7. Pair of carpels attached to a single stalk: note adaxial orientation of sutures with respect to floral axis, and remains of styles (S9191), ×2.—8. Two bud-scales (arrows) at the base of a broken inflorescence (S12387), ×2.—9. Inflorescence showing a distinct joint (arrow) at the base of a pair of follicles (S13323), ×2.8.—10. Mature follicle showing twisted follicle stalk and abaxial orientation of suture with respect to infructescence axis (S12410B), ×2. Scale bars, 4 mm.



FIGURES 11–15. *Cercidiphyllum*-like plants from the Paleocene of southern England and western North America. Specimens prefixed v. are from Berkshire, southern England (Reading Beds, Woolwich and Reading Formation, upper Paleocene) and are in the collections of the Department of Palaeontology, British Museum

(Woolwich and Reading Formation) of southern England were originally described as *Carpolithus gardneri* by Chandler (1961). The original specimens and additional material have recently been reexamined in detail (Crane, 1984) and assigned to *Nyssidium arcticum* (Heer) Iljinskaya. There is no evidence to suggest that the infructescences from the Reading Beds were borne on short shoots. The most informative specimens (Figs. 11, 12) suggest instead that the infructescences were borne as part of a long shoot system. These specimens exhibit whorls of oval scars that we interpret as leaf scars (Figs. 11, 12; see also Chandler, 1961). Growth in *N. arcticum* from the Reading Beds apparently resulted in the periodic production of whorls or pseudowhorls of leaves. Some leaf whorls are not followed by the production of an inflorescence (e.g., lower whorls, Figs. 11, 12). Other whorls of scars apparently delimit the base of infructescences (e.g., upper whorl, Fig. 11), and suggest that long shoot growth in this species was frequently terminated by the production of an inflorescence from the apical bud. Occasional branching occurred between the whorls of leaves, but the precise relationship of this to leaf and axillary bud production is not clear.

The pistillate inflorescences of *N. arcticum* from the Reading Beds are unknown, but the most complete infructescences are up to 130 mm long with about 15 widely spaced follicles approximately 5–6 mm apart. The follicles were borne singly (Fig. 11), or in pairs (Fig. 14), on short side branches of the infructescence axis (Crane, 1984). The best preserved specimen from the Reading Beds (Fig. 11) shows a distinct joint between the follicle stalk and the side branch of the inflorescence axis. Frequently this is not visible in poorly preserved material. However, other specimens indicate that follicles broke away from the infructescence axis at this point of weakness (Fig. 14). As in *Joffrea,* the ventral sutures of pairs of follicles face each other. Suture orientation in single follicles is often unclear, but at least some were probably oriented abaxially with respect to the infructescence axis at maturity (Crane, 1984).

Trochodendrocarpus arcticus (Heer) Kryshtofovich (Paleocene, U.S.S.R.)

Trochodendrocarpus arcticus (Heer) Kryshtofovich from the lower Paleocene (Danian) of Amur, eastern U.S.S.R. (Krassilov, 1973, 1976, 1977) is known from large specimens showing shoots that have attached infructescences. The infructescences are widely spaced and borne alternately, perhaps helically, on long shoots (Figs. 16, 17). A scar is often visible where each infructescence is attached to the long shoot (Figs. 16, 17). These scars are large and in the size range of petiole bases of associated *Cercidiphyllum*-like leaves. We suggest that the scars are those of alternate leaves and that each infructescence developed from an axillary bud. An alternative interpretation would be that each "infructescence" is a side branch of a large paniculate infructescence (Krassilov, 1977). This interpretation is more difficult to reconcile with the structure of other Paleocene *Cercidiphyllum*-like plants that are currently known.

The infructescences are up to 40 mm long and bear eight to 14 closely spaced follicles at distances of approximately 2–4 mm (Fig. 16). The follicles were borne singly (Krassilov, 1976, pl. 23: fig. 5) or in pairs (Fig. 18). None of the Amur material shows a distinct joint between the infructescence axis and the follicle stalk, although some of the dispersed follicles appear to have become detached at this point (Krassilov, 1976, pl. 24: fig. 9). The orientation of ventral sutures in the follicles is unclear.

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(Natural History). Specimens prefixed PP are from Decker, Montana (Tongue River Member, Fort Union Formation, upper Paleocene) and are in the paleobotanical collections of the Field Museum of Natural History, Chicago.—11. *Nyssidium arcticum* (Heer) Iljinskaya, long shoot with attached infructescences: note whorls of oval leaf scars (W) and distinct joint (J) between the follicles and infructescence axis (v.15336), ×1.—12. *N. arcticum,* long shoot with attached infructescence: note whorls of oval leaf scars (W) (v.60847), ×1.—13. *Cercidiphyllum*-like plant from Decker, Montana: note joint (J) between the follicle and infructescence axis, scars (arrows) where follicles have abscissed, and the abaxial orientation of the follicle suture with respect to the infructescence axis (PP34177), ×3.—14. *N. arcticum* showing a pair of follicles attached to a common stalk (v.60851), ×1.5.—15. *Cercidiphyllum*-like plant from Decker, Montana, showing joint (J) between the follicle and the infructescence axis, and scar of an abscissed follicle (upper arrow): note the abaxial orientation of the follicle suture with respect to the infructescence axis (PP34178), ×2.7. Scale bars, 5 mm.

FIGURES 16–18. *Trochodendrocarpus arcticus* (Heer) Kryshtofovich from the lower Paleocene of Amur, U.S.S.R.—16. Long shoot with attached infructescences: note scar at arrow, ×1.—17. Long shoot with attached infructescences: note scars at arrows, ×0.6.—18. Pair of follicles with facing sutures attached to a common stalk, ×1. Scale bars, 10 mm. Illustrations courtesy of V. Krassilov.

DISCUSSION

Shoot growth and phyllotaxy. *Cercidiphyllum* and its fossil relatives exhibit considerable variation in shoot growth. Long and short shoot differentiation is known in both *Joffrea speirsii* and extant *Cercidiphyllum,* but these short shoots are of quite different types. Those of *Joffrea* are similar to those found in some gymnosperms (e.g., *Ginkgo*) and many flowering plants (e.g., *Prunus*), which involve small growth increments

of an otherwise normal monopodial shoot. The sympodial short shoots of *Cercidiphyllum* are more unusual and less common in flowering plants as a whole. The extant vesselless dicotyledon *Tetracentron sinense,* often interpreted as closely related to *Cercidiphyllum* (Takhatajan, 1969), also exhibits this unusual sympodial short shoot growth (Bailey & Nast, 1945; Nast & Bailey, 1945). In *Nyssidium arcticum* from southern England and *Trochodendrocarpus arcticus* from Amur, short shoots are unknown.

Phyllotaxy in the fossil and Recent plants is as diverse as shoot growth, ranging from alternate to opposite to whorled. Leaf morphology in extant *Cercidiphyllum* is extremely variable (Brown, 1939; Swamy & Bailey, 1949; Chandrasekharam, 1974) and is further complicated by pronounced differences between long and short shoot leaves. Latest Cretaceous and early Tertiary *Cercidiphyllum*-like leaves exhibit extreme variation in shape and venation (Hickey, 1977; Wolfe, 1966). Some of these leaves may have been produced by genera only distantly related to *Cercidiphyllum,* but much of the variation may also be accounted for by the wide range of shoot growth patterns and phyllotaxy in fossil *Cercidiphyllum*-like plants.

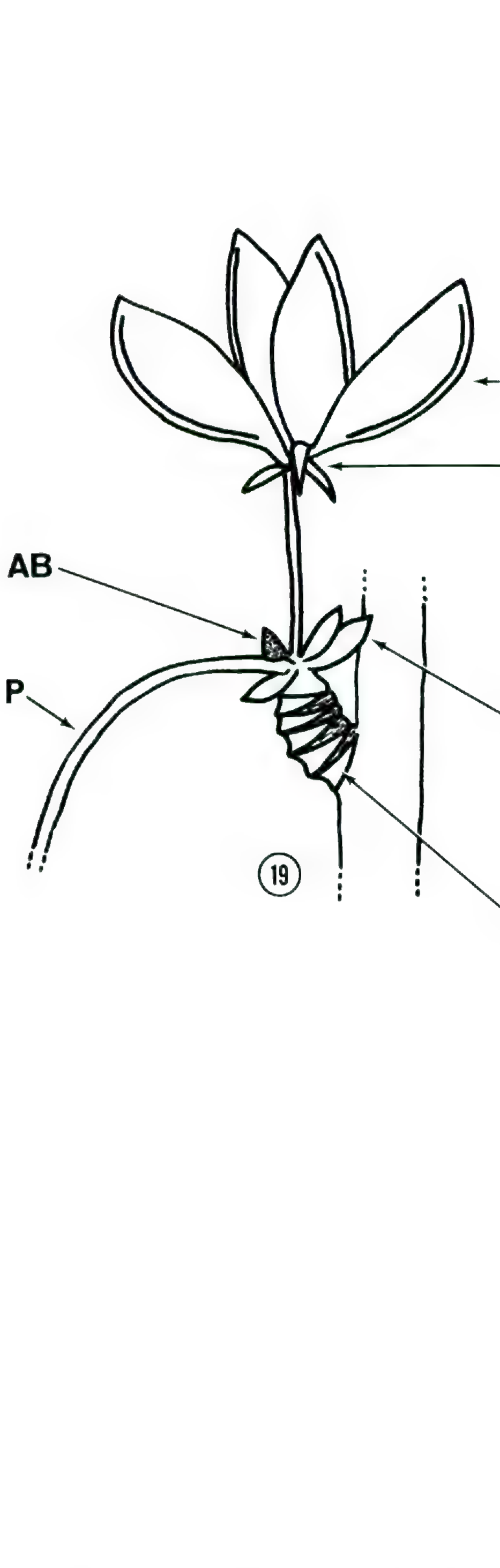
Inflorescence production and organization. Inflorescence production in *Cercidiphyllum* and its fossil relatives is highly variable (Table 1), but there is now a clear basis for directly interpreting the organization of the inflorescence in several fossil taxa in terms of the inflorescence of extant *Cercidiphyllum* (Figs. 19–24). In both the fossil and extant plants the inflorescence is a raceme. The joint between the branch of the inflorescence or infructescence axis and the stalk of the carpel or follicle is comparable to the joint at the base of each follicle in extant *Cercidiphyllum.* In extant *Cercidiphyllum* this joint marks the attachment point of a bract, and a bract may also have been borne at this point in the fossil plants (B, Figs. 19, 20). The joint is clear in *Joffrea* and *Nyssidium arcticum* but inferred in *Trochodendrocarpus arcticus.* The joint is also clearly visible in other early Tertiary material from North America (Figs. 13, 15), and we suggest that it was a general feature of Upper Cretaceous and early Tertiary *Cercidiphyllum*-like plants.

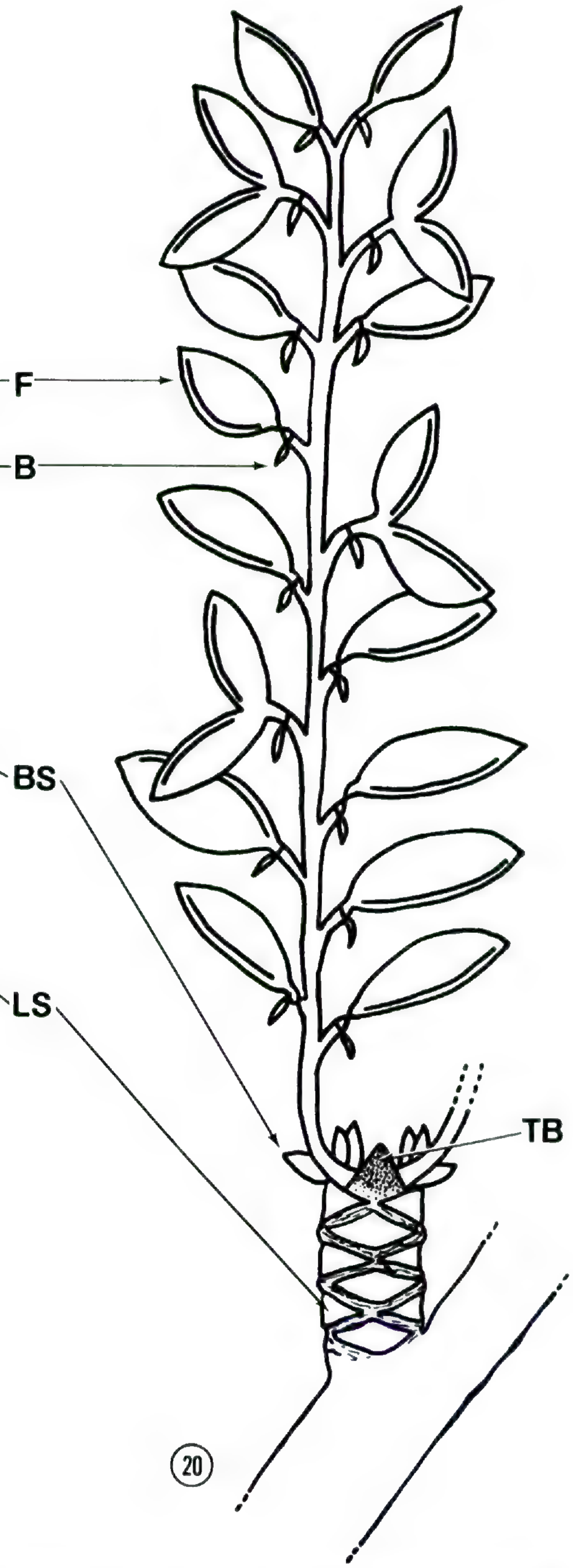
In *Joffrea speirsii* the base of the inflorescence has associated bud-scales (BS, Figs. 19, 20) that are comparable to those that surround the inflorescence, leaf and new axillary bud in extant *Cercidiphyllum.* These bud-scales have not been seen in the fossil material from southern England or Amur.

Under the interpretation given above, the inflorescences of the fossil plants are directly comparable to the inflorescences of extant *Cercidiphyllum,* and the homologies hypothesized by Brown (1939) and Swamy and Bailey (1949) are supported and considerably clarified. The differences between the fossil and Recent inflorescences are principally quantitative and concern the interrelated factors of inflorescence length, follicle number, and follicle crowding.

Suture orientation. The orientation of the suture in fossil material has frequently been difficult to determine (Crane, 1984; Hickey, 1977), and discussions of this feature are complicated by the need to distinguish between suture orientation with respect to the inflorescence axis and suture orientation with respect to the floral axis. In *Joffrea,* suture orientation can be compared in both inflorescences and infructescences. At carpel stage all the sutures of single carpels are clearly adaxially oriented with respect to the inflorescence axis, but in paired carpels the sutures face each other and their orientation with respect to the inflorescence axis is unknown. At maturity the stalk of single follicles often twists to orient the suture abaxially with respect to the infructescence axis. This may be related to dispersal of seeds from the follicles (Crane & Stockey, 1985), and the same phenomenon may have occurred in other North American early Tertiary material (Brown, 1939, pl. 55: figs. 3, 10). In upper Paleocene material from Decker, Montana, single follicles also have the suture oriented adaxially with respect to the infructescence axis (Figs. 13, 15), but in these cases the lack of obvious twisting suggests that the suture orientation at carpel stage may also have been adaxial. The variability of suture orientation in different early Tertiary plants, combined with developmental changes, such as occur in *Joffrea,* probably account for the different suture orientations recorded in the literature (Basinger & Dilcher, 1983; Crane, 1984; Hickey, 1977).

Several explanations have been offered to account for the suture orientation in extant *Cercidiphyllum* (Harms, 1916; Hutchinson, 1964; Leróy, 1980; Solereder, 1899; Swamy & Bailey, 1949). Based on the interpretation of the *Cercidiphyllum* inflorescence as an apocarpous flower, Hutchinson (1964) suggested that the apparently abaxial suture orientation was anomalous





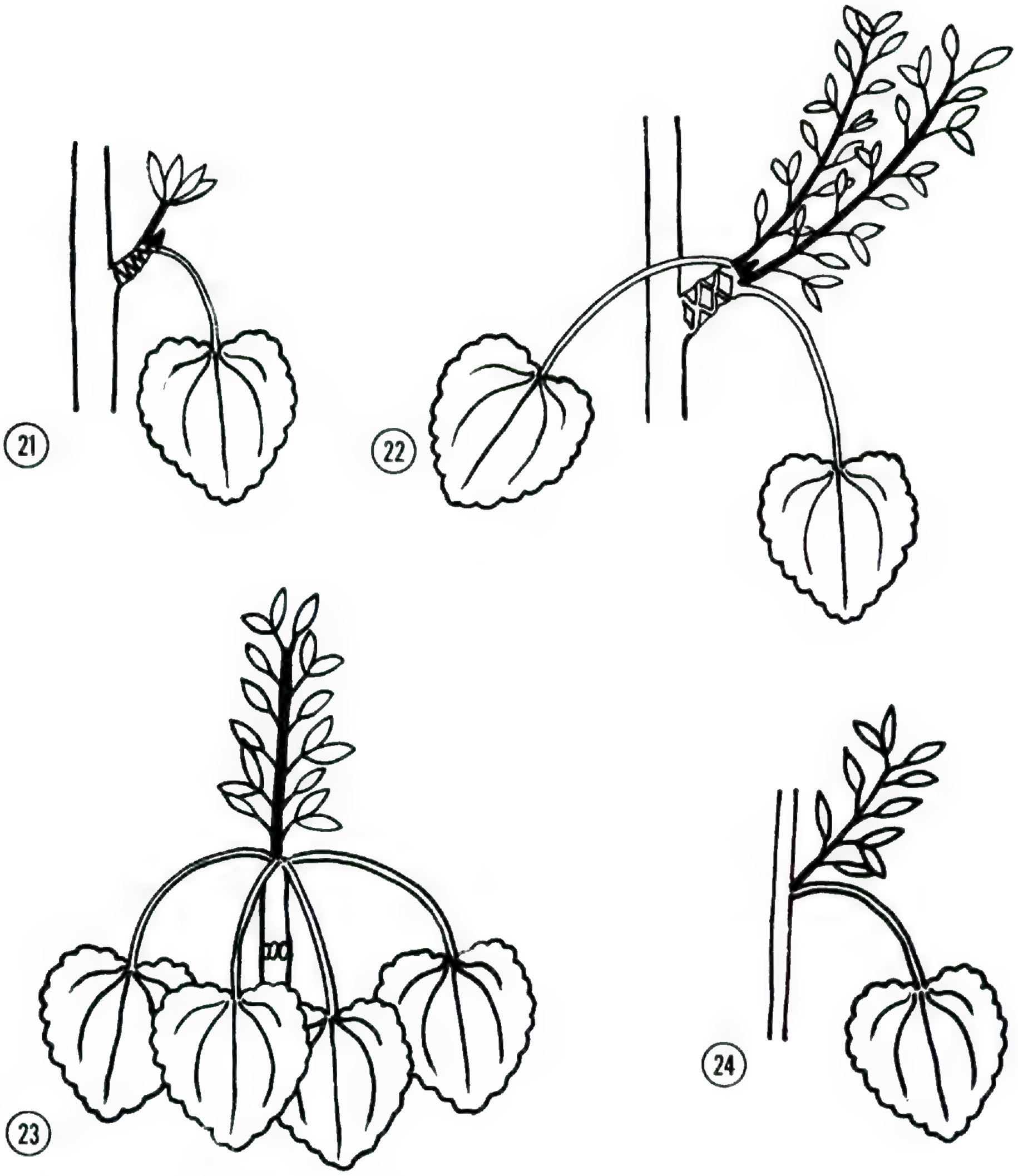
FIGURES 19, 20. Interpretative drawings showing homologous structures in the infructescences of *Cercidiphyllum* and *Joffrea*.—19. *Cercidiphyllum japonicum* Sieb. & Zucc. Short shoot with infructescence.—20. *Joffrea speirsii* Crane & Stockey. Short shoot with infructescence. AB = axillary bud, B = bract, BS = bud scale, F = follicle, LS = leaf scar, P = petiole, TB = terminal bud.

TABLE 1. Comparison of extant *Cercidiphyllum* with fossil *Cercidiphyllum*-like plants. See text for details of interpretations.

	Cercidiphyllum (Extant)	*Joffrea speirsii* (Paleocene, Canada)	*Nyssidium arcticum* (Paleocene, England)	*Trochodendrocarpus arcticus* (Paleocene, U.S.S.R.)
Shoots	Long shoots, sympodial short shoots	Long shoots, monopodial short shoots	Long shoots, short shoots absent?	Long shoots, short shoots absent?
Phyllotaxy	Opposite, subopposite, or whorled on long shoots, single on short shoots	Opposite (occasionally alternate?) on long shoots, opposite on short shoots	Whorls or pseudowhorls	Alternate
Position of inflorescence	Terminal on sympodial short shoots	In leaf axils on monopodial short shoots	Terminal on long shoots	In leaf axils on long shoots
Inflorescence type	Raceme	Raceme	Raceme	Raceme
Maximum length of infructescence	25 mm	130 mm	130 mm	40 mm
Follicle number per infructescence	2–8	ca. 40	ca. 15	8–14
Follicle orientation with respect to infructescence axis	Always abaxial	Single follicles, adaxial initially, some twisted and abaxial at maturity; unknown in paired follicles	Single follicles, ?adaxial, some abaxial at maturity; unknown in paired follicles	Unknown
Follicle number per flower	Always 1	1 or 2	1 or 2	1 or 2
Follicle orientation with respect to floral axis[a]	?Adaxial	?Adaxial, certainly adaxial when paired	?Adaxial, certainly adaxial when paired	Unknown

[a] Follicle orientation with respect to floral axis is difficult to assess in unicarpellate flowers.

and due to twisting of the carpels. This is not supported by detailed developmental studies or by carpel and follicle vasculature (Swamy & Bailey, 1949). The complex explanations of Harms (1916) and Leróy (1980) both involve transformation of a bud-scale on a vegetative shoot into a carpel, the single leaf of the shoot being transformed into a bract (Harms, 1916) or being lost (Leróy, 1980). Solereder's (1899) view is more straightforward, simply involving the loss of one of a pair of carpels that originally had opposite ventral sutures (adaxial with respect to the floral axis) and were oriented perpendicular to the inflorescence axis. This interpretation receives some support from the variable vascular supply to *Cercidiphyllum* carpels: some carpels have the dorsal vein supplied by a single vascular bundle from the stele, whereas others are supplied by two vascular bundles which fuse in the base of the carpel (Swamy & Bailey, 1949: 192, fig. 12). Equally significant however is the regular occurrence of pairs of follicles that have opposite ventral sutures in the inflorescences of *Joffrea, N. arcticum,* and *T. arcticus* (Figs. 6, 7, 14, 18). Although it is unknown whether the paired carpels and follicles are perpendicular or transverse with respect to the inflorescence axis, in all other respects the fossil plants conform to the archetype



FIGURES 21–24. Interpretative summary drawings showing shoot morphology, phyllotaxy, and infructescence position in extant and fossil Cercidiphyllaceae.—21. *Cercidiphyllum japonicum* (extant), showing sympodial short shoot with a single leaf, axillary bud, and terminal infructescence.—22. *Joffrea speirsii* (Paleocene) showing monopodial short shoot with opposite and decussate leaves, terminal bud, and axillary infructescences.—23. *Nyssidium arcticum* (Paleocene) from southern England showing long shoot with whorled leaves and terminal infructescence.—24. *Trochodendrocarpus arcticus* (Paleocene) from Amur showing long shoot with alternate leaves and an axillary infructescence.

of extant *Cercidiphyllum* envisaged by Solereder. Fossil infructescences more similar to those of extant *Cercidiphyllum* are first recorded from the Oligocene (Jähnichen et al., 1980).

CONCLUSIONS

Extinct latest Cretaceous and early Tertiary *Cercidiphyllum*-like plants are very diverse in phyllotaxy, shoot growth, pistillate inflorescence production, and the number and crowding of follicles per infructescence (Figs. 21–24). This extreme morphological diversity emphasizes that the complex of plants that produced *Cercidiphyllum*-like leaves during the latest Cretaceous and early Tertiary was highly heterogeneous, and further variations other than those considered here remain to be described in detail (Basinger & Dilcher, 1983). Extreme caution will therefore be necessary in assigning isolated and poorly understood organs of these *Cercidiphyllum*-like plants either to the extant genus or to already established and relatively well understood fossil plants such as *Joffrea*. The precise systematic relationships among these fossil plants remain to

be resolved by detailed studies of well-preserved inflorescences and shoots. Nevertheless, despite the structural diversity of *Cercidiphyllum*-like plants, the direct comparability of the inflorescences of extant *Cercidiphyllum* to those of the fossil *Cercidiphyllum*-like plants is now established. The fossils also provide support for the hypothesis that the suture orientation in extant *Cercidiphyllum* is due to loss of one of a pair of opposite carpels. The suture in extant *Cercidiphyllum* is therefore abaxial with respect to the inflorescence axis but probably phylogenetically adaxial with respect to the floral axis of the "ancestral" flower.

The recognition that bicarpellate flowers may be the primitive condition in the Cercidiphyllaceae strengthens the idea that the family may be closely related to the Hamamelidaceae (Cronquist, 1981). The close resemblance among the infructescences of *Joffrea, Nyssidium,* and *Trochodendrocarpus* and the racemes of unisexual, often apetalous, bicarpellate flowers seen in *Sinowilsonia* (Hamamelidaceae, Endress, 1977) is particularly striking. The phylogenetic relationships between the extant and fossil Cercidiphyllaceae and Hamamelidaceae deserve detailed study aimed at determining whether bicarpellate flowers constitute an important defining character for this group.

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FRUIT AND SEED DISPERSAL AND THE EVOLUTION OF THE HAMAMELIDAE[1]

BRUCE H. TIFFNEY[2]

ABSTRACT

The assumptions (1) that the Hamamelidae attained their zenith in the Cretaceous and, (2) that abiotic dispersal dominated in Cretaceous angiosperms, suggest that dispersal mode could be used as a character in evaluating families questionably associated with the Hamamelidae. A review of modern dispersal characters indicates that most "lower" Hamamelids are abiotically dispersed, but that several putatively derived families (e.g., Fagaceae, Moraceae) predominantly possess biotic dispersal. In many cases the dispersal mechanisms of a family are the same in the fossil record and the present day. However, in the Juglandaceae and Fagaceae the fossil record indicates a switch in dominance from abiotic to biotic dispersal around the Cretaceous-Tertiary border. Circumstantial fossil and modern evidence suggests a similar transition in the Moraceae/Cecropiaceae/Urticaceae and possibly the Ulmaceae. Thus, modern dispersal mode may not reflect the primitive dispersal mode in a lineage. Fossil dispersal evidence supports assignment of the Juglandaceae and Fagaceae to the Hamamelidae. Circumstantial evidence suggests abiotic dispersal is plesiomorphic in the Urticaceae and in the Moraceae/Cecropiaceae/Urticaceae complex: further evidence is required. Several results are noteworthy evolutionarily: (1) dispersal modes are malleable and can change within lineages; (2) this emphasizes the importance of mosaicism in angiosperm evolution; (3) the fossil and modern records suggest that families dominated by biotic dispersal are more diverse than families dominated by abiotic dispersal; (4) the Cretaceous-Tertiary boundary marks a time of major change in dispersal mode in the angiosperms; (5) the primitive fruit morphology of the Urticales appears to be the achene; and (6) derivation of fleshy structures from extra-ovarial tissues plays an important role in the dispersal of many species of the Moraceae, Cecropiaceae, and Urticaceae.

BACKGROUND AND HYPOTHESIS

The Hamamelidae are increasingly recognized as having been significant in the early history of the angiosperms. Members of the group have been traced to the Early Cretaceous (e.g., Doyle & Hickey, 1976; Hickey & Doyle, 1977) and in the earliest portions of the Late Cretaceous (Schwarzwalder & Dilcher, 1981); it is possible that the group may have had a separate origin from the Magnoliidae (Nixon, unpubl. data). Similarly, evidence for the importance and diversity of Hamamelidae in Cretaceous floras is growing. In particular, Leo Hickey (unpubl. data) has suggested, on the basis of fossil leaves, that the Hamamelidae reached a zenith of diversity in the Cretaceous and, with certain exceptions, have decreased in importance to the present day (see Cronquist, 1981: 153).

The fossil record of the angiosperms also reveals a pattern in relative sizes of diaspores. Cretaceous fruit and seed floras are dominated by small diaspores (1–3 mm on largest axis). Tertiary fruit and seed floras contain similarly small diaspores but also possess many much larger ones (Tiffney, 1984). As a broad generalization, small fruits and seeds may be abiotically or biotically dispersed, whereas large fruits and seeds are more often biotically dispersed. The small size of the Cretaceous angiosperm diaspores, together with the general absence of modern dispersal agents, suggests that Cretaceous angiosperms were largely abiotically dispersed. The extraordinary diversification of birds, bats, and terrestrial mammals in the early Tertiary (see Tiffney, 1984) provided biotic dispersal agents that are important in angiosperm biology today. These animals moved larger seeds than would abiotic means and were contributing factors to the evolution of modern angiosperms forming closed-canopy, late-successional forests such as those found in the warm-temperate and tropical areas of the world today (Tiffney, 1984). In sum, this scenario

[1] I thank Michael Zavada and David Dilcher (Indiana University) for the opportunity to examine this topic through their invitation to participate in the Symposium on the Hamamelidae, Leo Hickey for information on the leaf fossil record and for his criticisms throughout the gestation of this paper, and three reviewers for their detailed and constructive criticisms. Research was partially supported by the United States National Science Foundation grant BSR-8306002.

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suggests that Cretaceous angiosperm groups should be dominated by abiotic dispersal, and that biotic dispersal should be significant only in groups that either evolved in the Tertiary or altered their dispersal biology during that period.

If the assumption that the Hamamelidae are primarily a Cretaceous group is correct, then all "true" Hamamelidae should show fossil or recent evidence of abiotic dispersal. In theory, this provides one test of hypotheses on the systematic affinities of certain families [e.g., Juglandaceae (Hickey & Wolfe, 1975)] whose association with the Hamamelidae has been questioned. Families dominated by biotic dispersal mechanisms would presumably have affinities outside the Hamamelidae, whereas those with abiotic dispersal mechanisms are at least not disqualified from the sub-class. However, this conclusion rests on the further assumption that the primary dispersal mode within a family has not changed over time.

The reader is cautioned that, while focused on dispersal, this paper carries no implication that dispersal biology is more (or less) important than any other character in elucidation of the phylogeny of the Hamamelidae.

Methods and Materials

In this paper, I follow Cronquist (1981) for disposition of families within the sub-class Hamamelidae and Willis (1973) for generic composition of the families.

Data on the modern modes of dispersal and associated information (Table 1) were assessed at the generic and occasionally the specific level, and were compiled from the following sources: Engler and Prantl (1894), Prain (1917), Standley (1920–1926, 1928), Engler and Prantl (1930), Ridley (1930), Standley and Steyermark (1946), Lawrence (1951), Martin et al. (1951), Standley and Steyermark (1952), Hutchinson and Dalziel (1954), Vink (1957), Jacobs (1960), Backer (1963), Hutchinson (1964), Melchior (1964), Owhi (1965), Hutchinson (1967), Radford et al. (1968), van der Pijl (1969), Miller (1971), Willis (1973), Walker (1976), Montgomery (1977), Soepadmo (1977), Croat (1978), Heywood (1978), Chang (1979), Kuang and Lu (1979), Li and Cheng (1979), Anonymous (1980), Elias (1980), Ming (1980), Wiggins (1980), Cronquist (1981), Dassanayake and Fosberg (1981). These sources are cited specifically only where warranted. In families possessing more than one dispersal mode, the relative contribution of the different modes is expressed as a percentage of the total number of genera or species within the family. Cases in which dispersal mode is not recorded in the literature, or where it appeared equivocal or generalized in light of fruit or seed morphology, are noted individually.

The fossil record of angiosperm fruits and seeds is good in the Tertiary (Tiffney, 1977) but scanty in the Cretaceous. Only a few fruits and seeds of the Hamamelidae are known from the Cretaceous, although the record of the group is much better in the Tertiary. The appearance of modern dispersal agents roughly at the Cretaceous-Tertiary boundary presumably had a substantial effect on fruit and seed morphology, and may have influenced the appearance of "modern" characters. The absence of modern fruit and seed taxa in the Cretaceous may also partially be an artifact of scientific interest. Only within the last 15 years have researchers seriously examined Cretaceous angiosperm fruit and seed floras (e.g., Knobloch, 1971, 1977; Friis, 1983, pers. comm.; Knobloch & Mai, 1984; Tiffney, unpubl. data).

The fossil record of the families of the Hamamelidae is summarized in Figure 1. Figures 2–8 summarize the history of families with many genera reported from the fossil fruit and seed record. The data come from the primary literature and are taken from a file on the occurrences of fossil fruits and seeds that I have been assembling as a parallel to Muller's (1981) summary of the fossil pollen records of modern families.

The generic identifications are accepted as given by the primary authors. I have excluded some clearly erroneous reports but have not examined every occurrence in detail. In some cases this may be misleading. For example (Tiffney, in prep.), it may prove impossible to separate the seeds of many modern genera of the Hamamelidaceae in the fossil record. Thus, the reports of individual genera of Hamamelidaceae in Figure 2 may be misleading. Similarly, biases of preservation, mosaic evolution, and the attitudes of examining scientists may result in the placement of extinct forms in modern genera, or may cloud the recognition of modern genera in the fossil record.

Stratigraphic locations are taken as reported by primary authors except where clearly in error. Localities from western North America are dated from Evernden and James (1964) and Wolfe (1981). Period and Epoch durations are based on the time scale of Harland et al. (1982).

The summary of dispersal patterns in the fossil

TABLE 1. Characters of diversity, dispersal, distribution, habit, ecology, and pollination for the families of the Hamamelidae sensu Cronquist (1981). See text for sources.

Family	Number Genera/ Species	Genera Abiotically Dispersed	Dispersal Morphology	Genera Biotically Dispersed
Tetracentraceae (1)	1/1	100%	winged seed	0
Trochodendraceae (2)	1/1	100%	winged seed	0
Cercidiphyllaceae (3)	1/2	100%	winged seed	0
Eupteleaceae (4)	1/2	100%	winged fruit	0
Platanaceae (5)	1/6, 7	100%	hairy achene or nutlet	0
Hamamelidaceae (6)	28/100+	100%	winged seeds (18%) ballistic seeds (82%)	0
Myrothamnaceae (7)	1/2	100%	tiny seeds in capsule	0
Daphniphyllaceae (8)	1/35	0	fleshy drupe	100%
Didymelaceae (9)	1/2	0	large drupaceous fruit?	100%
Eucommiaceae (10)	1/1	100%	winged fruit	0
Barbeyaceae (11)	1/1	100%	nut with large accrescent sepals	0
Ulmaceae (12)	18/150	33%	winged fruits and fleshy to semi-fleshy drupes	67%
Cannabaceae (13)	2/3	unclear—the bracts aid in wind dispersal, but Ridley (1930) records animal dispersal		
Moraceae (14)	51/1,333	8% genera (13% spp.)	dry achenes, some drupes, many pseudo-drupes	78% genera (86% spp.)
Cecropiaceae (15)	8/275	0	pseudo-drupes from fleshy floral parts	100%
Urticaceae (16)	46/1,255	37% genera (66% spp.)	abiotic via dry achene, ballistic, or winged fruit biotic via drupes, pseudo-berries, receptacle-fruit, sticky surfaces, and eliasomes	47.5% genera (29% spp.)
Leitneriaceae (17)	1/1	100% (?)	dry, possibly floating, drupe	0
Rhoipteleaceae (18)	1/1	100%	winged nut	0
Juglandaceae (19)	9/60	56% genera (37% spp.)	winged nut or drupaceous	44% genera (63% spp.)
Myricaceae (20)	3/50	unclear—no particular adaptations exist, and both abiotic and biotic dispersal observed		
Balanopaceae (21)	1/9	0	acorn-like drupe	100%
Fagaceae (22)	8/800	0	nut within cupule; rarely mildly winged	100%
Betulaceae (23)	6/120	83%	nut or samara	17%
Casuarinaceae (24)	1/50	100%	samaroid	0

TABLE 1. Continued.

Distribution	Habit	Deciduous/ Evergreen	Dioecious/ Monoecious	Dispersal Unit	Pollination Mode
Nepal, China, Burma	tree	D	perfect	seed	anemophily
Korea, Japan, Taiwan	tree	E	androdioecious	seed	secondarily anemophily
China, Japan	tree	D	dioecious	seed	anemophily
China, Japan, Assam	tree	D	perfect to protandrous	fruit	anemophilous, some entomophily
Mediterranean to Himalayas, Assam; Mexico to Canada	tree	D	monoecious	fruit	anemophily
subtropical to temperate regions, Old and New Worlds	trees and shrubs	D & E	perfect or unisexual	seed	primarily entomophily
Africa, Madagascar	small shrub	?	dioecious	seed	anemophily
E Asia, Malaysia	trees or shrubs	?	dioecious	fruit	?
Madagascar	tree	E	dioecious	fruit	? anemophily
China	tree	D	dioecious	fruit	anemophily
NE Africa, Arabia	small tree	?	dioecious	fruit	anemophily
tropical and temperate Northern Hemisphere	trees, shrubs, and vines	D & E	monoecious or perfect	fruit	anemophily
N temperate to tropical	herbs	—	monoecious or dioecious	fruit	anemophily
widespread, largely tropical	trees, shrubs, and vines	D & E	monoecious or dioecious	fruit or "fruit" of floral parts	anemophily, some entomophily
tropical	trees, shrubs, and vines	?	rarely monoecious, commonly dioecious	fruit or "fruit" of floral parts	anemophily, some entomophily
tropical and subtropical, temperate	herbs, shrubs, vines, and trees (but mostly herbs)	—	monoecious, dioecious, and polygamous	fruit or "fruit" of floral parts	anemophily
SE United States	shrub to small tree	D	dioecious	fruit	anemophily
SW China, Vietnam	tree	D	perfect, sometimes unisexual	fruit	anemophily
Northern Hemisphere	trees	D	monoecious	fruit	anemophily
temperate and tropical, Old and New Worlds	shrubs	D & E	monoecious	fruit	anemophily
SW Pacific, New Caledonia	tree	E	dioecious	fruit	anemophily
cosmopolitan, except Africa	trees and shrubs	D & E	monoecious, seldom dioecious, rarely perfect	fruit	anemophilous, secondarily entomophilous in some species
temperate Northern Hemisphere	trees and shrubs	D	monoecious	fruit	anemophilous
SW Pacific, Australia, Indomalesia	trees and shrubs	E	monoecious	fruit	anemophilous

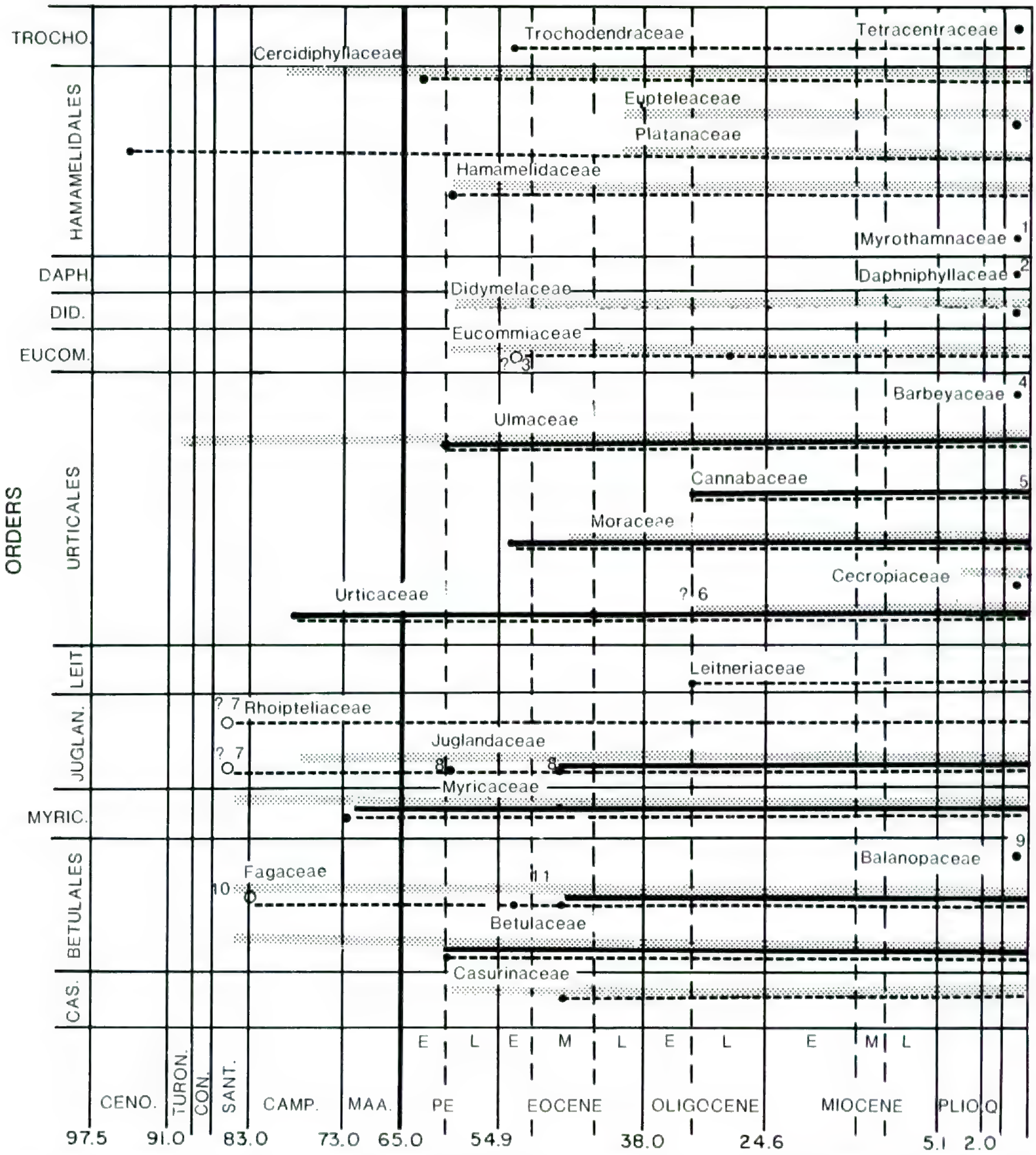

FIGURE 1. First-occurrence data for families of the Hamamelidae sensu Cronquist (1981) based on fossil fruits, seeds, and pollen. Solid line, record of biotic dispersal within a family; dotted line, record of abiotic dispersal within a family; grey line, first occurrence data for pollen (after Muller, 1981). CENO. = Cenomanian, TURON. = Turonian, CON. = Coniacian, SANT. = Santonian, CAMP. = Campanian, MAA. = Maastrichtian, PE = Paleocene, PLIO = Pliocene, Q = Quaternary, E = Early, M = Middle, L = Late. Absolute dates after Harland et al. (1982). Trocho. = Trochodendrales, Daph. = Daphniphyllales, Did. = Didymelales, Eucom. = Eucommiales, Leit. = Leitneriales, Juglan. = Juglandales, Myric. = Myricales, Cas. = Casuarinales. Notes: (1) Abiotically dispersed; (2) Biotically dispersed; (3) *Eucommia*-like fruits of the early Eocene, Pierce and Hickey (pers. comm.); (4) Abiotically dispersed; (5) Cannabaceae appear to have "generalized" dispersal mechanisms; (6) Muller (1981) suggested possible Oligocene pollen of Urticaceae; (7) Friis (1983) reported fruits that conform most closely to those of the Juglandaceae but also possess similarities with those of the Myricaceae and Rhoipteleaceae; (8) *Casholdia, Polyptera,* and *Cyclocarya,* all wind dispersed, appear in the Upper Paleocene. The first animal-dispersed fruit of the family is *Juglans,* which appears in the Middle Eocene; (9) Biotically dispersed; (10) Tiffney and Friis have unpublished floral and fruiting material similar to Fagaceae from Martha's Vineyard, Massachusetts, United States. The identification requires verification; (11) *Fagopsis* (wind dispersed) appears in the Early Eocene; *Quercus* and possibly *Trigonobalanus* (animal dispersed) appear in the Middle Eocene.

record is based only on fossil fruit and seed records. Mosaic evolution (e.g., Manchester, 1981a; Knoll et al., 1984; Stebbins, 1984) dictates that it is inappropriate to infer a modern dispersal mechanism on the basis of a fossil leaf or pollen grain belonging to a modern genus. In these descriptions, when no reference is cited for a specific conclusion (e.g., that the morphology of the seeds of *Tetracentron* suggests abiotic dispersal), the conclusion is that of the present author.

Results

Tetracentraceae. The fruit is a follicetum, dehiscing to release small seeds with spongy, wing-like outgrowths (Cronquist, 1981; Lawrence, 1951). The size and wings suggest abiotic dispersal.

Takhtajan (1974) placed Cretaceous specimens of *Nordenskioldia* Heer in the Trochodendrales, but there is no reason to accept these as members of either the Trochodendraceae or Tetracentraceae. The same reference also places *Nyssidium* Heer in the Trochodendrales, but Crane (1984a) demonstrated the affinities of many fossils assigned to this genus with the Cercidiphyllaceae (see below).

Trochodendraceae. The fruit is a follicetum, dehiscing to release many quite small seeds. The seed size suggests abiotic dispersal.

Reid and Chandler (1933) described *Trochodendron*(?) *pauciseminum* Reid & Chand. from the Early Eocene London Clay flora of England. The identification was given with a question mark, and is based on five- to six-loculed, septicidal fruits containing small seeds with (wing-like) extensions. If the identification is correct, then *Trochodendron* was abiotically dispersed in the Eocene.

Cercidiphyllaceae. The separate follicles bear small, asymmetrically-winged seeds. Wind dispersal is reported in the literature and borne out by personal observation.

The follicles of *Cercidiphyllum* are fairly common fossils (e.g., Brown, 1939; Jähnichen et al., 1980; Crane, 1984a). The oldest presently verified fruit record is from the Paleocene (Brown, 1962; Crane, 1984a). However, Crane (1984a) demonstrated that many fruits assigned to the form genus *Nyssidium* Heer represent the Cercidiphyllaceae, and reports of *Nyssidium* extend back to the Turonian (Takhtajan, 1974; see also Krasilov, 1976). Thus, fruits of the family could be present in the Late Cretaceous. It is likely that the Cercidiphyllaceae were more diverse in the Late Cretaceous and early Tertiary. Crane and Stockey (1985) describe an extinct multi-organ assemblage as the genus *Joffrea* Crane & Stockey from Late Paleocene sediments: while varying in other characters, its seeds are very similar to those of *Cercidiphyllum.* Seeds found with fossil *Cercidiphyllum* follicles (Reid & Chandler, 1933; Crane, 1984a) resemble the seeds of the extant species, suggesting wind dispersal.

Eupteleaceae. The fruits are small samaras or winged nutlets adapted for wind dispersal. No fossil fruits are reported.

Platanaceae. The infructescence is a globose head of densely hairy achenes or nutlets that are shed at maturity. The hairs increase surface area, and the fruits may be wind dispersed or float on water.

Schwarzwalder and Dilcher (1981) described Cenomanian-age leaves and infructescences from Kansas that they suggest belong in the Platanaceae. Friis (1984) reported platanaceous inflorescences from the Late Cretaceous of North Carolina and Sweden. Hickey (pers. comm.) indicated that "*Platanus*-like" infructescences occur in the Lower Cretaceous sediments of the Potomac Group (see Hickey & Doyle, 1977). These records suggest that the Platanaceae are the oldest family of the Hamamelidae represented by fruiting remains. The morphology of the individual fruits is often similar to that of the fruits of modern *Platanus,* suggesting abiotic dispersal, although Manchester (1986) notes an Eocene *Platanus* with slightly larger fruits lacking the pappus-like hairs of the modern genus. These fruits are still quite small (2–3 mm) and Manchester (pers. comm.) suggests that they are probably abiotically dispersed.

Hamamelidaceae (Fig. 2). The majority of genera possess a ballistic dispersal mechanism in which the seed is "squirted" out from the fruit by pressures created in the fruit wall by moisture loss (e.g., *Hamamelis* L.). However, in the Altingioideae (*Altingia* Nor., *Liquidambar* L.) the seeds are very small and occasionally possess wings [although Vink (1957) noted that the oily seeds of *Altingia* have been observed to attract monkeys, birds, and ants]. Similarly, in the Hamamelidoideae, *Exbucklandia* R. W. Brown possesses large, winged seeds indicative of wind dispersal, and *Rhodoleia* Champ. ex Hook. has small, disk-like seeds dispersed by wind.

Both *Liquidambar* and the extinct genus *Steinhauera* Presl appear in the Paleocene (Chandler,

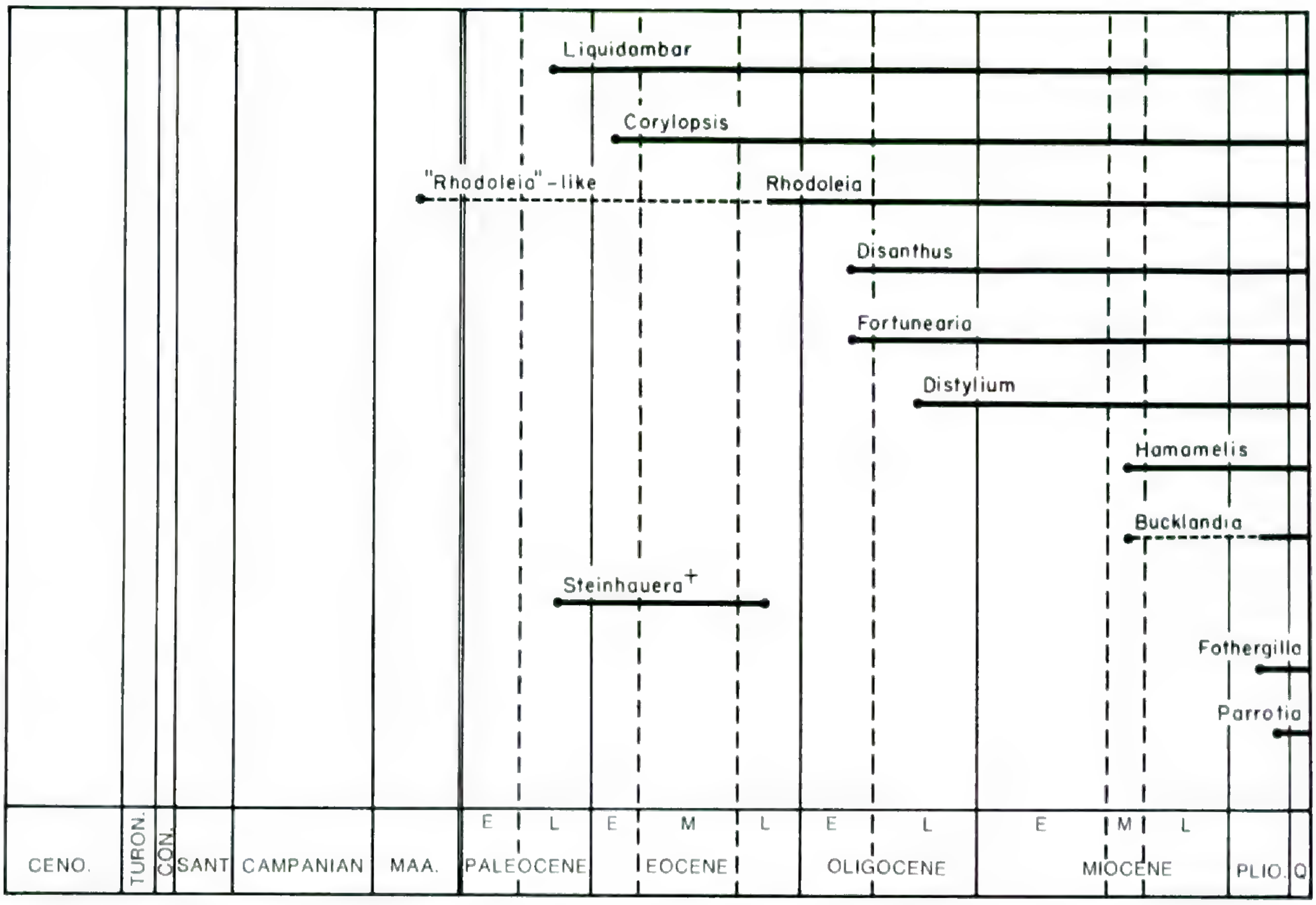

FIGURE 2. First-occurrence data for genera in the Hamamelidaceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. *Liquidambar* L., Chandler (1961b); *Corylopsis* Sieb. & Zucc., Chandler (1961b); "*Rhodoleia*-like" (*Klikovispermum* Knob. & Mai), Knobloch and Mai (1984); *Rhodoleia* Champ., Mai and Walther (1985); *Disanthus* Maxim., Mai and Walther (1978); *Fortunearia* Rehdr. & Wils., Mai and Walther (1978); *Distylium* Sieb. & Zucc., Takhtajan (1974); *Hamamelis* L., Zablocki (1930); *Bucklandia* R. Br. ex Griff., first possible appearance, Brown (1946), later possible appearances, Reid and Reid (1915), Szafer (1946); *Fothergilla* L., Szafer (1946, 1954); *Parrotia* C. A. Mey., Tralau (1963); *Steinhauera* Presl, Mai (1968).

1961b; Mai, 1968; Collinson, unpubl. data). The shape of the fruits and seeds suggests wind dispersal. Knobloch and Mai (1984) drew a comparison between the fossil seed *Klikovispermum waltheri* Knobl. & Mai from the Maastrichtian of Czechoslovakia and the seeds of *Rhodoleia* Champ., but the first clear report of *Rhodoleia* is provided by Mai and Walther (1985) in the Late Eocene. Ballistically-dispersed members of the Hamamelidaceae first appear in the Early Eocene (*Corylopsis* Sieb. & Zucc., Chandler, 1961b), followed in the Oligocene by *Disanthus* Maxim., *Fortunearia* Rehder & Wilson (both reported by Mai & Walther, 1978), and *Distylium* Sieb. & Zucc. (Takhtajan, 1974). There is no evidence in the fossil record that the Hamamelidaceae were ever anything but wind or ballistically dispersed.

Myrothamnaceae. The fruit is a dehiscent capsule bearing many seeds (Cronquist, 1981), which Willis (1973) states are small. This suggests abiotic dispersal, but specific evidence is lacking. There is no fossil record of the fruits of the family.

Daphniphyllaceae. The fruit is a one-seeded, fleshy, indehiscent drupe that is black or green at maturity and about 1 cm long (Ridley, 1930; Walker, 1976; Cronquist, 1981). The fruit characters suggest biotic dispersal. There is no fossil record of the fruits of this family.

Didymelaceae. The fruit is "a large one-seeded drupe, with lateral grooves (as in *Prunus*)" (Willis, 1973). The morphology is suggestive of biotic dispersal. There is no fossil record of the fruits of this family.

Eucommiaceae. The fruit is a large samara, similar in shape to those of *Ailanthus* Desf. or *Fraxinus* L. Wind dispersal is indicated.

The oldest clear fossil is of *Eucommia krystofovichii* Negru from the Middle Miocene of Moldavia (Takhtajan, 1974). However, Brown (1940) reported samaras of *Eucommia montana* Brown from the ? Upper Oligocene of western North America (see note under Ulmaceae). The

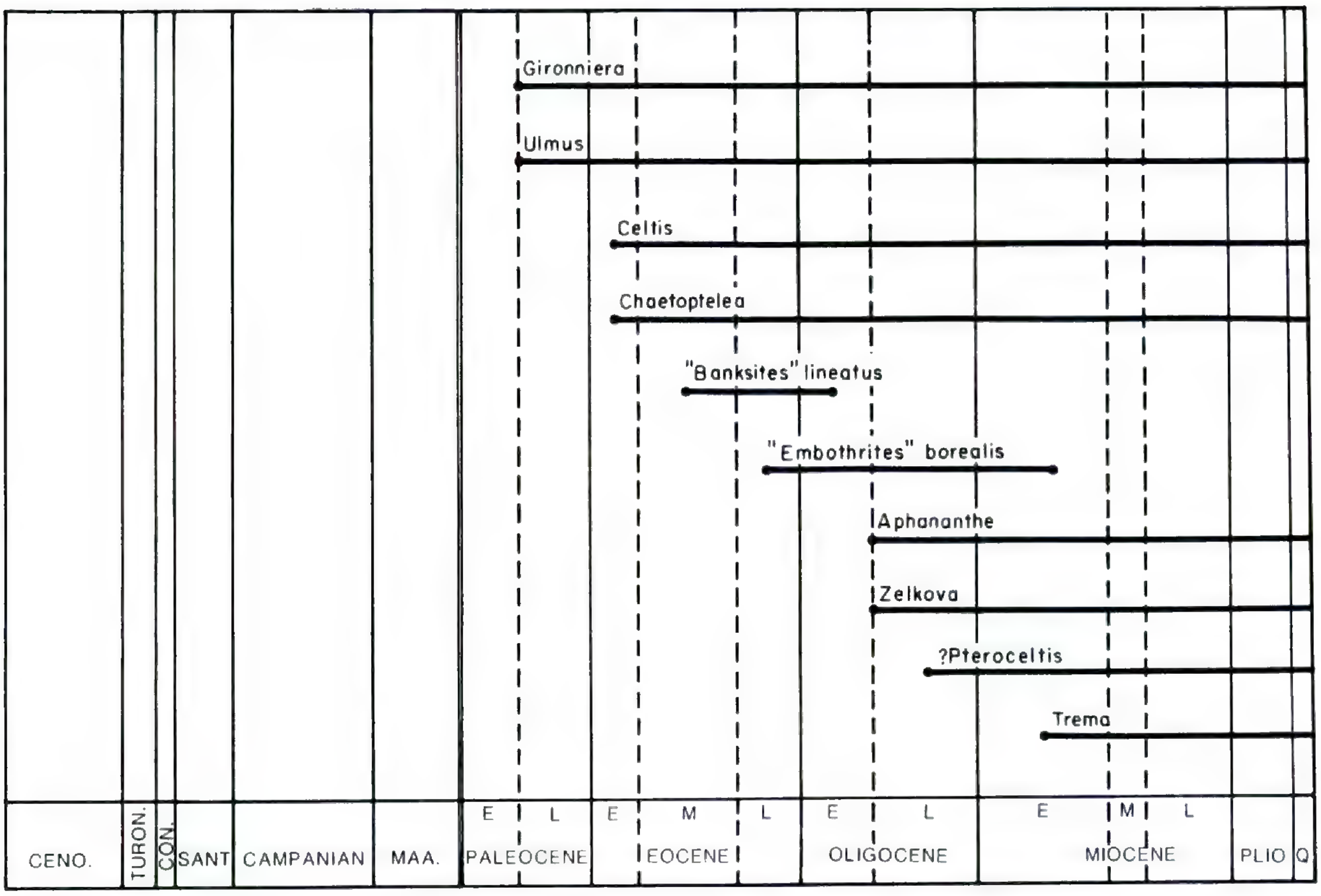

FIGURE 3. First-occurrence data for genera in the Ulmaceae based on fossil fruits and seeds. Conventions as in Figure 1. *Gironniera* Gaudich., unpublished data cited in Mai and Gregor (1982); *Ulmus* L., first report Brown (1962), next report Givulescu (1980); *Celtis* L., unpublished specimens provided by Leo J. Hickey; *Chaetoptelea* Liebm., MacGinitie (1941); "*Banksites*" *lineatus* Unger, Manchester (in prep.); *Embothrites borealis* Unger, Manchester (in prep.); *Aphananthe* Planch., Takhtajan (1982); *Zelkova* Spach., Chandler (1957); ? *Pteroceltis* Maxim., first report Weyland (1937), questioned by Kirchheimer (1957); *Trema* Lour., Holý (1975).

latter fruits are shorter and broader than those of modern *Eucommia* and might constitute an extinct genus. Similarly, Pierce and Hickey (pers. comm.) are investigating a samara from the Paleocene of western North America that is similar to the fruits of the modern genus but differs in several specifics. The last two reports hint at a greater taxonomic diversity in the family in the early Tertiary and underscore the importance of wind dispersal in the group.

Barbeyaceae. The fruit is a "short-beaked nut with associated accrescent, somewhat membranous, prominently veined sepals" (Cronquist, 1981). In some species the length of the sepals exceeds that of the nut by 2:1 (Prain, 1917). These morphological characters suggest wind dispersal, although animal predation and dispersal of the nut could not be excluded. There is no fossil record of the fruits of this family.

Ulmaceae (Fig. 3). The Ulmoideae (five genera) possess wind-dispersed samaras, with the exception of *Planera* J. F. Gmel, which has a fleshy fruit. The Celtidoideae (ca. 12 genera) possess fleshy-walled, animal-dispersed, drupes with the exception of *Pteroceltis* Maxim., which has a winged fruit, and *Chaetacme* Planch., which has a tiny, hard-surfaced drupe (Hutchinson, 1967). Twenty-six percent of the species of the family are abiotically-dispersed samaras and 74% are drupes presumed to be biotically dispersed.

Fruits of the two subfamilies appear in the fossil record at approximately the same time. The Ulmoideae are first represented by *Ulmus* L., which appears in the Paleocene of western North America (Brown, 1962), although this record may include some material of *Eucommia* (P. Crane, pers. comm.). *Chaetoptelea* Liebm. appears in the Early Eocene of western North America (MacGinitie, 1941), and the extinct form "*Banksites*" *lineatus* Unger appears in the Middle Eocene of the same area, persisting to the Early Oligocene (Manchester, in prep.). The extinct form "*Embothrites borealis*" Unger appears in the Upper Eocene of Europe and persists through the Early Miocene (Manchester, in prep.).

The Celtidoideae are first represented by en-

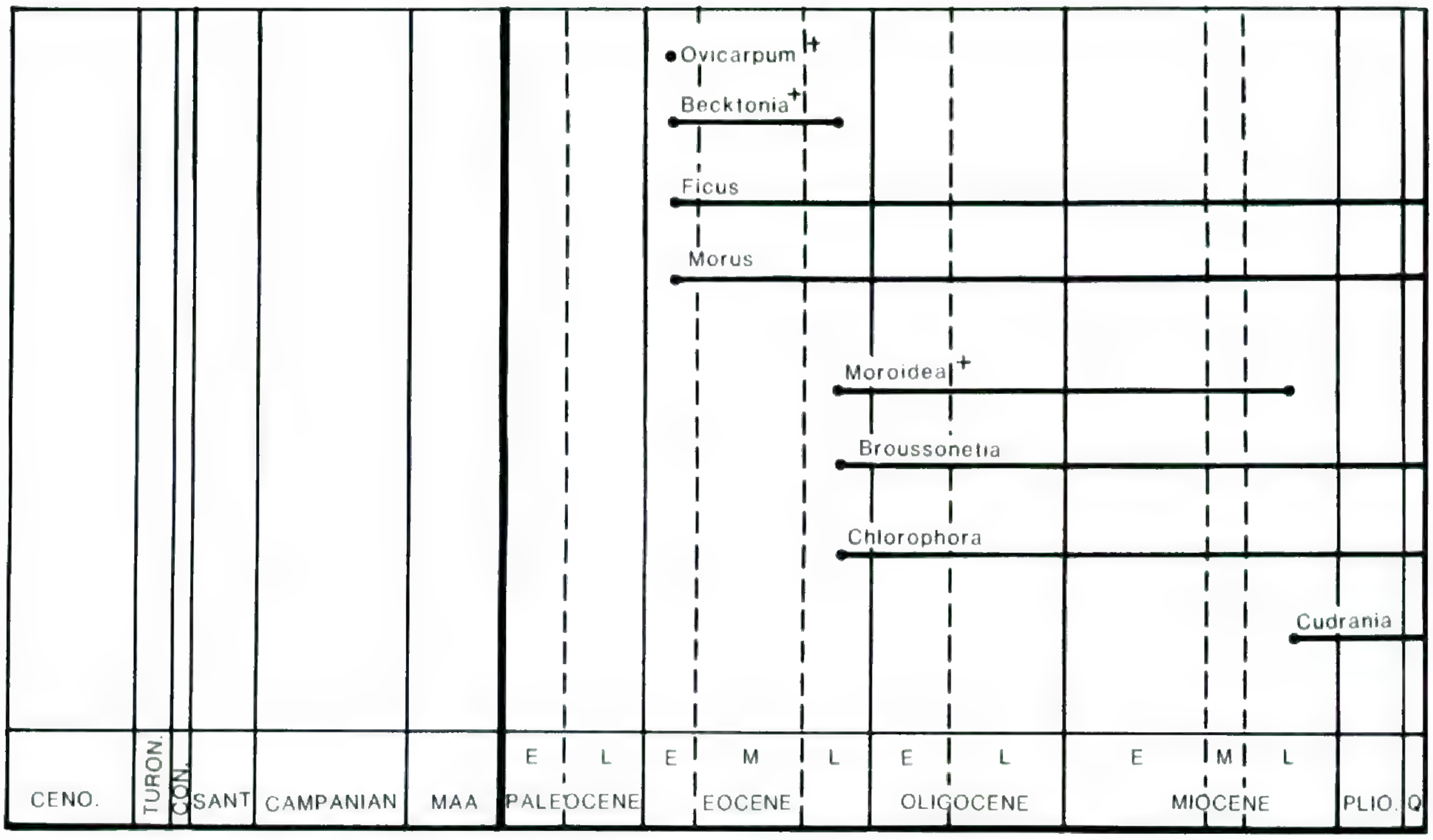

FIGURE 4. First-occurrence data for genera in the Moraceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. *Ovicarpum* Chandler, Chandler (1962); *Becktonia* Chandler, first report Chandler (1963), last report Chandler (1961a); *Ficus* L., Chandler (1962); *Morus* L., Chandler (1961b); *Moroidea* Chandler, first report Chandler (1961a), last report Palamarev (1971); *Broussonetia* L'Hérit. ex Vent., Chandler (1925–1926, 1961a); *Chlorophora* Gaudich., Chandler (1925–1926, 1961a); *Cudrania* Trécul, Palamarev (1968).

docarps of *Gironniera* Gaudich., in the Paleocene of Europe (unpubl. data cited in Mai & Gregor, 1982). This is closely followed by endocarps of *Celtis* L. from the Early Eocene of western North America (Leo Hickey, pers. comm.). Only one more genus of the Ulmoideae appears, this in the Oligocene, compared to three more of the Celtidoideae; possibly two in the Oligocene and one in the Miocene. [Weyland's (1937) report of *Petroceltis* Maxim. has been questioned by Kirchheimer (1957).] This imbalance of subsequent appearances could be taken to reflect differential diversification of the two subfamilies; the Celtidoideae are more numerous in the present day.

Cannabaceae. The fruit is an achene invested to a greater or lesser degree in a persistent calyx. If large enough, the calyx wings permit wind dispersal in *Humulus* L., but often the wings are reduced and wind dispersal is impossible (Ridley, 1930). Animal dispersal is known in *Cannabis* L. (Ridley, 1930) and may be significant. Neither dispersal mechanism is dominant in either genus.

Dorofeev (in Takhtajan, 1982) reported four species of *Humulus* L. and two species of the extinct genus *Humularia* Dorof. [which requires a new name, as *Humularia* Duvign. (Leguminosae) has nomenclatural priority] as appearing in the Oligocene of western Siberia. The first report of *Cannabis* L. is in the Miocene of eastern Siberia (Dorofeev, 1969). The morphology of the fruits suggests no particular change from their present "generalized" dispersal adaptations.

Moraceae (Fig. 4). Out of 51 genera of Moraceae examined, 78% had fleshy diaspores and 8% had dry, presumably abiotically-dispersed fruits. I was unable to ascertain fruit type in 14%. At the species level, 86% of the diaspores are fleshy and 13% are dry. Based on the total sample of the fleshy-diaspore genera, only 11% are drupes (true fruits in which flesh is derived from the carpel wall), whereas over 67% are dispersal structures in which the flesh is provided by enlarged, accrescent floral parts or enlarged receptacles surrounding an achene. This pattern is clearer at the species level, where almost all fleshy diaspores are derived from perianth parts. Thus, although biotic dispersal adaptations strongly dominate in the Moraceae, the attractive diaspore structure does not develop from the true fruit, but from structures external to it. Floral parts also participate in abiotic dispersal. Ridley (1930) noted in *Sloetia sideroxylon* Teijsm. & Binneud ex Kurz. that the swollen sepals may squeeze the mature achene out of the floral remains with enough force to throw the achene a yard. In *Dorstenia* L., Ridley noted that drying of the receptacle and enclosed flowers creates

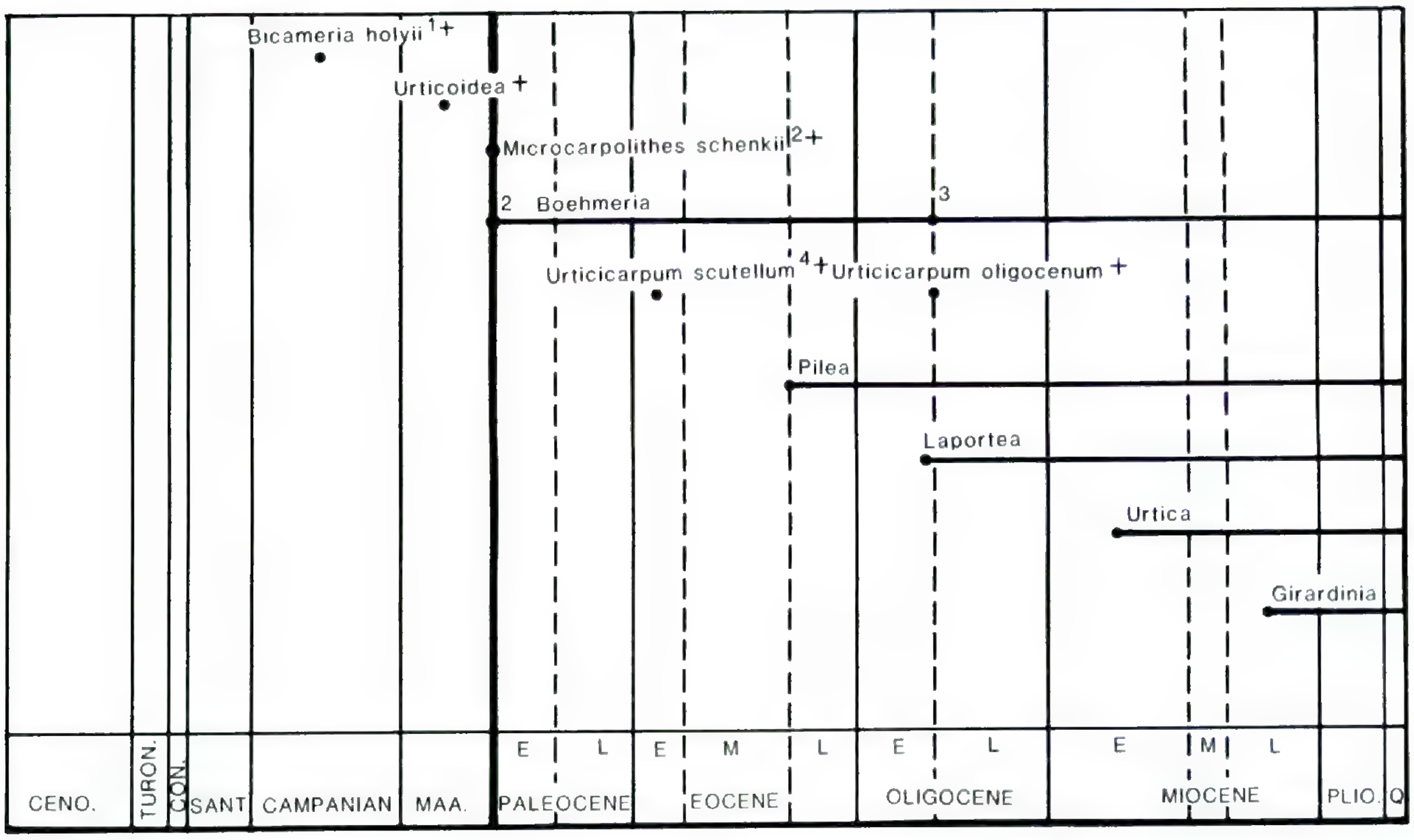

FIGURE 5. First-occurrence data for genera in the Urticaceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. Notes: (1) "Senonian" age assigned, this encompasses stages ranging from the Coniacian to Maastrichtian; (2) age given as Maastrichtian to Paleocene; (3) next report of *Boehmeria,* Takhtajan (1982); (4) affinities with the Urticaceae uncertain, *Bicameria holyii* Knobloch & Mai, Knobloch and Mai (1984); *Urticoidea* Knobloch & Mai, Knobloch and Mai (1984); *Microcarpolithes schenkii* Knobloch, Knobloch (1971); *Boehmeria* Jacq., Knobloch (1971); *Urticicarpum scutellum* Reid & Chandler, Reid and Chandler (1933); *Urticicarpum oligocenum* Dorof., Dorofeev (in Takhtajan, 1982); *Pilea* Lindl., Palamarev (1973); *Laportea* Gaudich., Mai and Walther (1978); *Urtica* L., Dorofeev (in Takhtajan, 1982); *Girardinia* Gaudich., Dorofeev (in Takhtajan, 1982).

enough pressure to "shoot" the achenes away from the plant.

Fig-like objects (*Ficus ceratops* Knowl.) have been reported from the Late Cretaceous of western North America but lack the internal structure and external morphologic detail necessary for secure systematic assignment. Shoemaker (1977) reviewed these fossils and placed them in the form genus *Carpites* Schimper. The first assured occurrence of this family is in the Early Eocene floras of southern England, where *Ficus* L. (Chandler, 1962), *Morus* L. (Chandler, 1961b), and two extinct genera, *Ovicarpum* Chandl. (Chandler, 1962) and *Becktonia* Chandl. (Chandler, 1963) are reported. This is followed by the appearance of *Broussonetia* L'Hérit ex Vent., *Chlorophora* Gaudich., and the extinct genus *Moroidea* Chandl. (all Chandler, 1961a) in the Late Eocene. These fossils largely are of achenes that could have been borne within a fleshy berry of the involucre or could have been dispersed dry. If one accepts the identifications of the modern genera (*Ficus, Morus, Broussonetia, Chlorophora*) as correct, biotic dispersal was dominant in the family from its first appearance.

Cecropiaceae. All eight genera possess fleshy diaspores indicative of animal dispersal. Similar to the Moraceae, the flesh in these diaspores is primarily derived from floral parts, rather than from the carpel wall. There is no fossil record of the fruits or seeds of this family.

Urticaceae (Fig. 5). As in the Moraceae, the basic fruit type is an achene, a small nut or rarely a drupe, and the floral parts play a strong role in dispersal. However, abiotic dispersal is common in this family; out of 46 genera, over 47% are biotically dispersed, about 37% abiotically dispersed, and data could not be obtained for 15%. The pattern is inverted at the species level. Almost 66% of the species are abiotically dispersed, over 29% biotically, and almost 5% unknown. Of the abiotically-dispersed genera, roughly half had mechanisms developed from the true fruit, whereas the other half had mechanisms dependent on accrescent floral parts forming wings, hairs, or aiding in ballistic dispersal. Of the biotically-dispersed genera, well over half are berry-mimics based on fleshy floral parts and one-third have sticky or hairy floral parts that are assumed to attach the fruit to animals. In one genus, the

floral parts appear to form an eliasome-mimic that attracts ants. Only three genera of animal-dispersed forms have true drupes.

The fossil record of the Urticaceae is "bipartite," with a cluster of largely extinct genera of fruits from the Cretaceous and early Tertiary, followed by the appearance of modern genera of fruits in the Oligocene. Knobloch and Mai (1984) relate *Bicameria holyi* Knobl. & Mai of the Senonian and *Urticoidea cucurbitoides* Knobl. & Mai of the Maastrichtian to the family, and Knobloch (1971) described *Microcarpolithes schenkii* Knobl. and *Boehmeria ctyrokyi* Knobl. from undifferentiated sediments ranging from Campanian to Paleocene in age. If the last identification is correct, then it is the oldest report of a modern genus in the group. If not, then the first is *Pilea* Lindl., which appears in the Upper Eocene (Palamarev, 1973), followed by *Boehmeria* Jacq. (Takhtajan, 1982), and *Laportea* Gaudich. (Mai & Walther, 1978) in the mid-Oligocene. As with the Moraceae, it is not possible to infer mode of dispersal from the morphology of the fruits. If one follows the dispersal modes of the modern genera in the fossil record (*Boehmeria, Pilea, Laportea, Urtica*), they are abiotically dispersed with the exception of *Boehmeria*.

Leitneriaceae. The fruit is a dry drupe with a leathery, slightly spongy exocarp. This could facilitate animal dispersal or, in light of the moist habitats in which *Leitneria* Chapm. grows, possibly aid in water dispersal.

Dorofeev (1963; recent stratigraphy from Takhtajan, 1982) reported *Leitneria venosa* (Ludwig) Dorof. from several Oligocene localities in western Siberia. No difference in dispersal mechanisms from the extant *L. floridana* Chapman can be inferred from the fossil.

Rhoipteleaceae. The two-winged samaroid nut is wind dispersed. See discussion under Juglandaceae for fossil record.

Juglandaceae (Fig. 6). The fruit is a nut, which may either be samaroid or drupaceous, corresponding to wind or animal dispersal. By species number, the drupaceous forms (*Carya* Nutt. and *Juglans* L.) outnumber the wind-dispersed ones about 2:1. Further details of dispersal in this family are provided in the section on the alteration of dispersal mode within families.

The oldest records of fruits with possible juglandalean affinity are of the form genera *Manningia* Friis, *Antiquocarya* Friis, and *Caryanthus* Friis from the Senonian of Sweden. While these flowers and fruits differ from those of extant Juglandaceae in some characters and in their size, and while they may be compared to modern flowers and fruits of the Myricaceae and Rhoipteleaceae in some respects, Friis (1983: 185–186) concluded "the best correlation of the fossil fruits and floral structures described here is with members of the Juglandaceae." Given this evidence, it seems best to recognize the fossils as closely associated with the precursors of modern Juglandaceae, if not actually representative of the family.

Cyclocarya Iljinskaja co-occurs in the upper Paleocene with the extinct genera *Polyptera* Manchester & Dilcher (both Manchester & Dilcher, 1982), *Casholdia* Crane & Manchester (Crane & Manchester, 1982), and the form genus *Juglandicarya* Reid & Chandler (Manchester, 1981a); all but the last-named are winged. This is followed by the appearance of the winged genera *Englehardtia* Leschen. ex Bl. (Jähnichen et al., 1977; Manchester, 1981a), *Platycarya* Sieb. & Zucc. (Chandler, 1964; Wing & Hickey, 1984), and *Pterocarya* Kunth. (Manchester & Dilcher, 1982) in the Early Eocene. The animal dispersed *Juglans* L. appears in the Middle Eocene (Manchester, 1981a), and *Carya* Nutt. appears at the Eocene-Oligocene border (Mai, 1981).

The Senonian fruits are quite small and show no sign of fleshy exocarps; features suggestive of abiotic dispersal. There is a clear transition in numerical dominance from wind-dispersed species to animal-dispersed species through the Tertiary (see Fig. 9 and discussion below).

Myricaceae. The fruit is drupaceous or almost a nutlet, sometimes enclosed by small bracteoles. As with the Cannabaceae, it is difficult to reach a satisfactory generalization about dispersal in the family. Ridley (1930) and Martin et al. (1951) noted that the fruits are dispersed by birds, but water and wind dispersal are also possible. In light of these observations, no single dispersal mode is assumed for this family.

The earliest report is of *Comptonia octocostata* (Knobl.) Knobl. from the early Maastrichtian of Europe (Knobloch, 1975; Jung et al., 1978). This is followed by *C. goniocarpa* Mai & Walther from the Early to mid-Oligocene of East Germany (Mai & Walther, 1978). *Myrica boveyana* (Heer) Chandl. appears in the Early Eocene of southern England (Chandler, 1961b) and is followed by a host of subsequent reports of other species. The

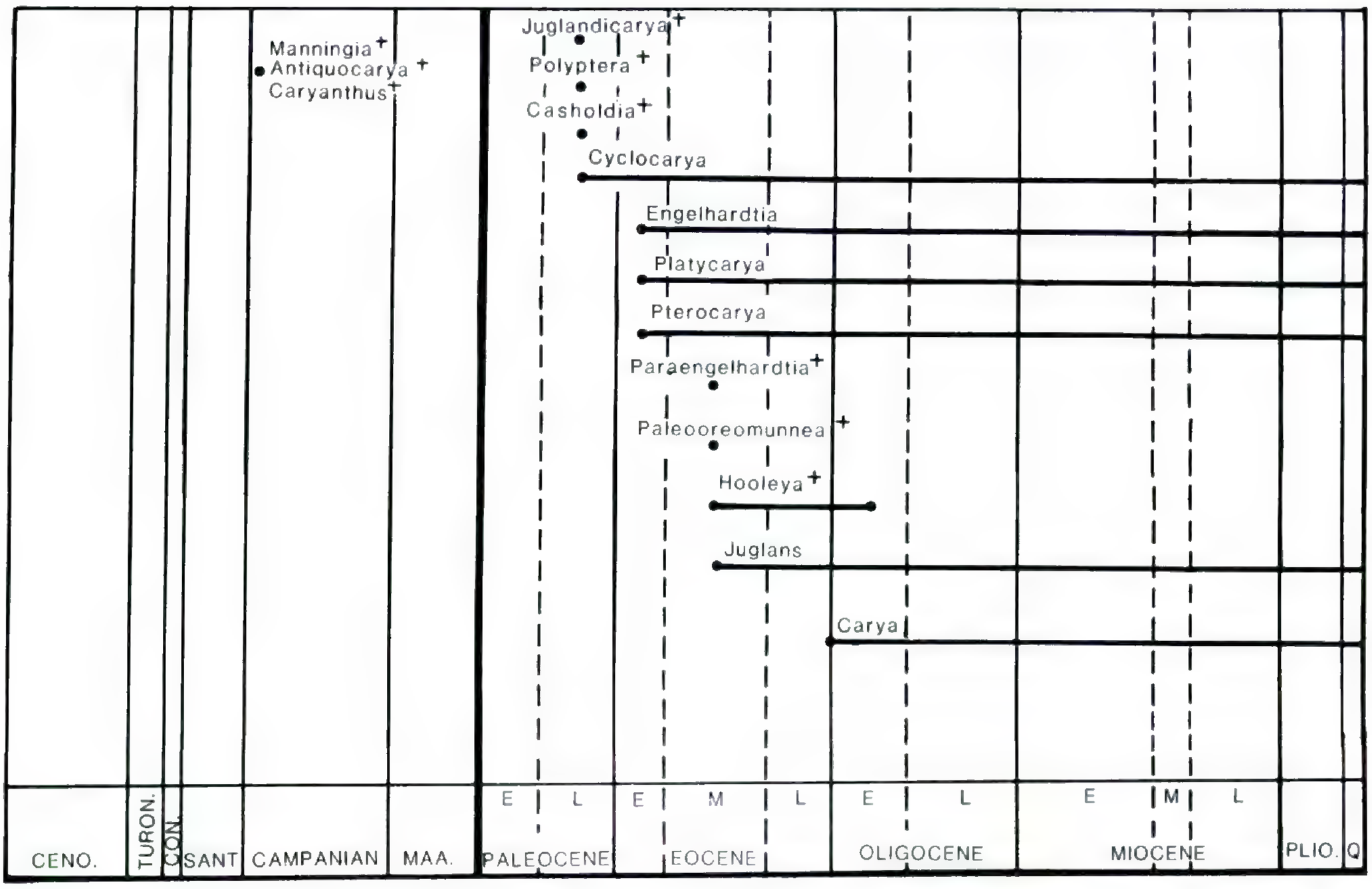

FIGURE 6. First-occurrence data for genera in the Juglandaceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. Although published sources of first occurrences are given, much insight comes from Manchester (1981a). *Manningia* Friis; *Antiquocarya* Friis; *Caryanthus* Friis, Friis (1983); *Juglandicarya* Reid & Chandler, Reid and Chandler (1933), Manchester (1981a); *Polyptera* Manchester & Dilcher, Manchester and Dilcher (1982); *Casholdia* Crane & Manchester, Crane and Manchester (1982); *Cyclocarya* Iljinskaja, Manchester and Dilcher (1982); *Engelhardtia* Leschen. ex Bl., Jähnichen et al. (1977), Manchester (1981a, note: Manchester placed all fossil Engelhardtioid fruits into the form genus *Palaeocarya* Saporta, as the range of variation seen in the fossils exceeds that in the modern genus sensu stricto. I retain *Engelhardtia* here as a more familiar concept, accepting that it may encompass several genera); *Platycarya* Sieb. & Zucc., Chandler (1964), Wing and Hickey (1984); *Pterocarya* Kunth, Manchester and Dilcher (1982); *Paraengelhardia* Berry, Dilcher et al. (1976); *Paleooreomunnea* Dilcher, Potter & Crepet, Dilcher et al. (1976); *Hooleya* Reid & Chandler, Wing and Hickey (1984); *Juglans* L., Brown (1962), Manchester (1981b); *Carya* Nutt., Mai (1981).

morphology of the fossils parallels that of the living species, suggesting a similar "generalized" dispersal syndrome in the past.

Balanopaceae. The fruit is a fleshy-walled, acorn-like drupe, sitting in an acorn-like cup (Willis, 1973; Cronquist, 1981). The fruit morphology suggests biotic dispersal. There is no fossil record of the fruits of this family.

Fagaceae (Fig. 7). The fruits are nuts, often of considerable size, indicating biotic dispersal. Only in *Nothofagus* Blume are samaroid fruits occasionally encountered, although Soepadmo (1977) noted that, in most species, they are large and disperse very poorly. The family may be considered biotically dispersed.

The oldest fruit of the family may be represented by reproductive material from the Santonian-Campanian of Massachusetts, United States. These most closely resemble miniaturized fruits of *Lithocarpus* Bl. in morphology (Tiffney & Friis, unpubl. data). This record requires validation. The extinct genus *Fagopsis* Hollick appears in the Early Eocene (Manchester & Crane, 1983), followed by *Trigonobalanus* Forman (Mai & Walther, 1978), *Quercus* L. (Bones, 1979; Manchester, 1981b), and possibly *Castanea* Mill. (Crepet & Daghlian, 1980) in the Middle Eocene. *Lithocarpus* Bl. may appear in the Late Eocene (Axelrod, 1966), although Manchester and Crane (1983) are dubious of this record. *Fagus* L. appears in both Europe (Chandler, 1957) and North America (Chaney, 1927; supported by Smiley & Huggins, 1981) in the mid-Oligocene.

The Cretaceous fossils are about 3 mm in diameter, show no signs of a fleshy covering, and occur in prodigious numbers, all suggestive of abiotic dispersal. *Fagopsis* is the earliest known Tertiary representative of the group and produces small fruits borne within wing-like cupules, often aggregated in rings, the whole ap-

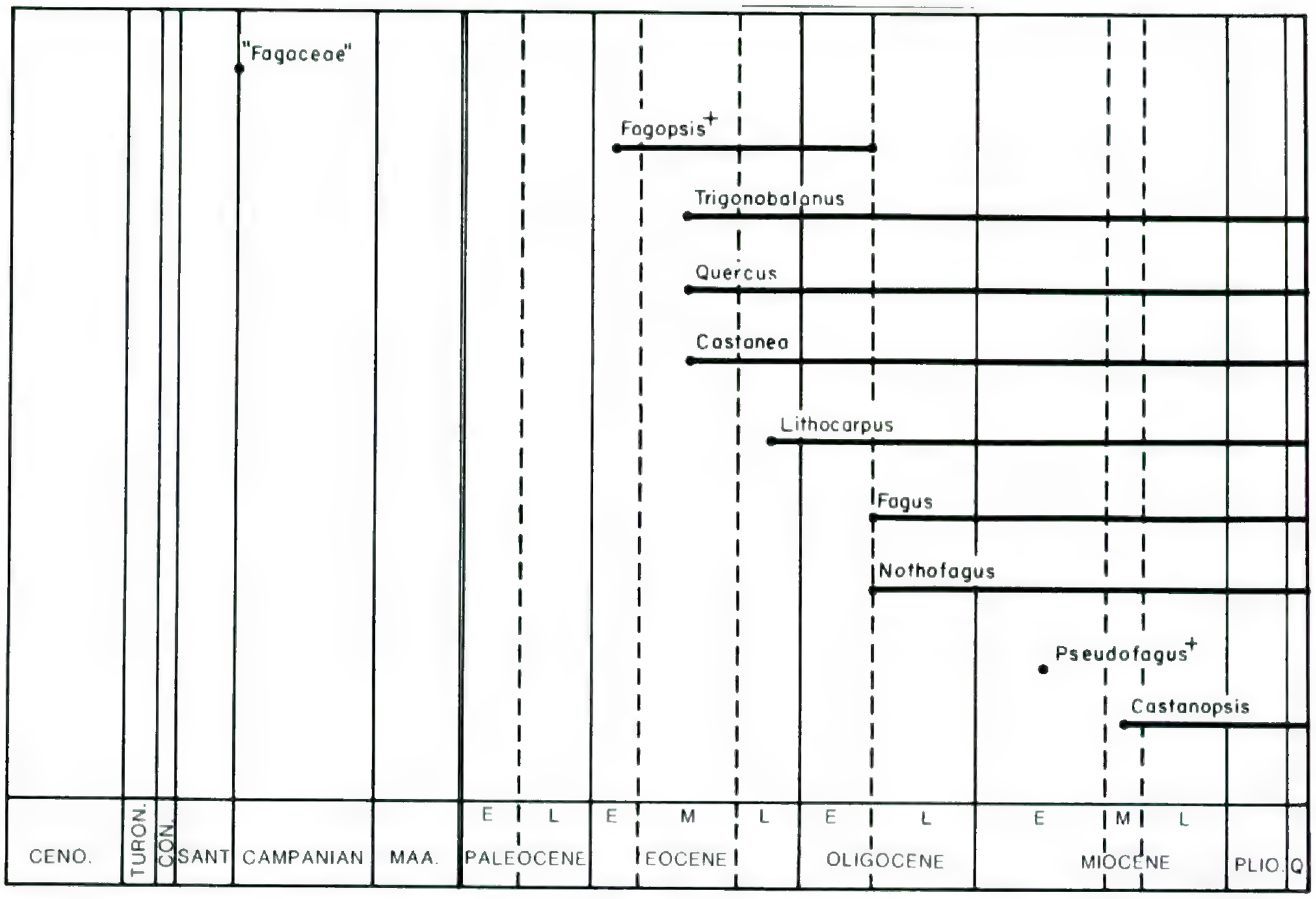

FIGURE 7. First-occurrence data for genera in the Fagaceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. "Fagaceae," possible fagaceous flowers and fruits under investigation by Tiffney and Friis; *Fagopsis* Hollick, Manchester and Crane (1983); *Trigonobalanus* Forman, Mai and Walther (1978); *Quercus* L., Manchester (1981b); *Castanea* Mill., Crepet and Daghlian (1980); *Lithocarpus* Bl., Axelrod (1966), see Manchester and Crane (1983); *Fagus* L., Chaney (1927), Chandler (1957); *Nothofagus* L., Hill (1983); *Pseudofagus* Smiley & Huggins, Smiley and Huggins (1981); *Castanopsis* (D. Don) Spach., Mai (1964); *Castanea* Mill., van der Burgh (1978).

parently adapted for wind dispersal. The other members of the family, including the extinct mid-Tertiary *Pseudofagus idahoensis* Smiley & Huggins (Smiley & Huggins, 1981), are animal dispersed.

Betulaceae (Fig. 8). Of the six living genera, the fruits of *Alnus* Mill. and *Betula* L. are wind dispersed. *Carpinus* L. and *Ostrya* Scop. fruits may be wind dispersed [Ridley (1930) gave evidence that they travel respectable distances], or the bracts may be too small to permit effective dispersal. Thus, animal dispersal may also be important in these genera (Ridley, 1930; Martin et al., 1951). *Corylus* L. generally has a nut too large to be wind-borne by its bracts and is often animal dispersed (Ridley, 1930). The dispersal mode in *Ostryopsis* Decne. is not reported in the literature. Illustrations of the fruit (Li & Cheng, 1979) show a relatively large fruit in a winged involucre. In sum, dispersal mechanisms intergrade from animal to wind in the family.

The oldest fossil records involve *Corylus* L. (Brown, 1962; Koch, 1978) from North America and Greenland and the extinct genus *Palaeocarpinus* Crane (Crane, 1981) from England and North America (Crane, 1984b), both appearing in the mid-Paleocene. In addition, Crane (1981) suggests that "*Atriplex*" *borealis* (Heer) Laurent of the Paleocene may also belong to the family. *Alnus* Mill. appears at the Paleocene/Eocene boundary (Takhtajan, 1982) and *Betula* L. in the Middle Eocene (Crane, 1984b). *Carpinus* L. may appear in the Late Paleocene (Chandler, 1961b), although Crane (pers. comm.) believes this record is of *Palaeocarpinus*, and that the first fossil fruit of *Carpinus* is of Late Eocene age (see Crane, 1981). With the exception of *Corylus*, all fossil members of the family are morphologically adapted to a greater or lesser degree for wind dispersal.

Casuarinaceae. The seed is a small, one-seeded samara, well-adapted for wind dispersal.

Christophel (1980) reported mature inflorescences of *Casuarina* Adans. from the Eocene of

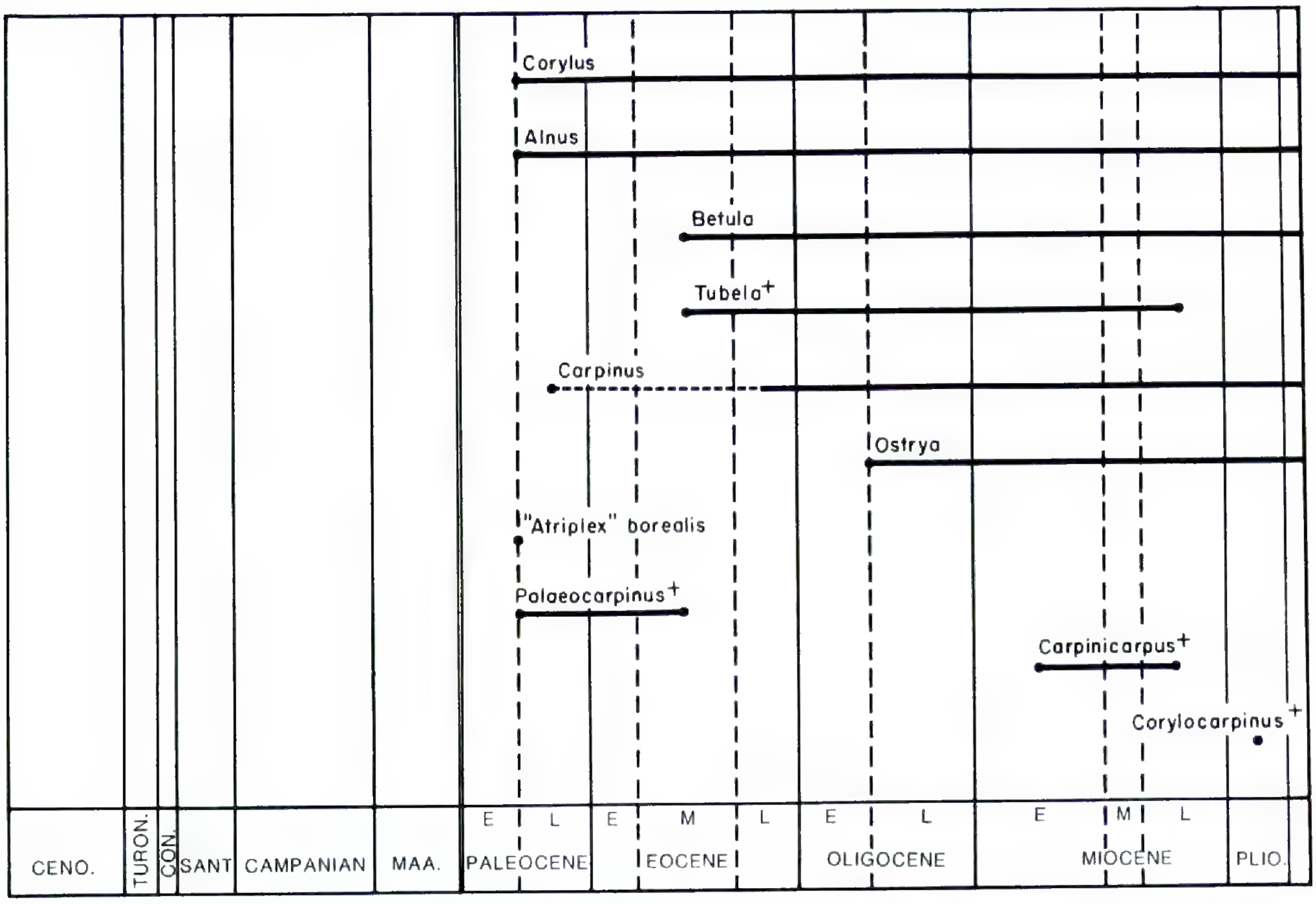

FIGURE 8. First-occurrence data for genera in the Betulaceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. *Corylus* L., Brown (1962), Koch (1978); *Alnus* Mill., P. Crane, (pers. comm.), first published report from Paleocene-Eocene border, Dorofeev (in Takhtajan, 1982); *Carpinus* L., Chandler (1961b), P. Crane (pers. comm.) suggested this may be *Palaeocarpinus* and that the earliest *Carpinus* fruit is Late Eocene; *Betula* L., Dorofeev (in Takhtajan, 1982); *Tubela* Dorof., Dorofeev (in Takhtajan, 1982); *Ostrya* Scop., Dorofeev (in Takhtajan, 1982); "*Atriplex*" *borealis* (Heer) Laurent, Crane (1981); *Palaeocarpinus* Crane, Crane (1981), Crane and Stockey (1986); *Carpinicarpus* Nikitin, Nikitin (1965); *Corylocarpinus* Straus, Straus (1969).

Australia that are virtually identical to those of modern species. This suggests that the Eocene members were also wind dispersed.

SUMMARY OF ABIOTICALLY-DISPERSED FAMILIES

The Trochodendraceae, Cercidiphyllaceae, Platanaceae, Myrothamnaceae, Eucommiaceae, Barbeyaceae, Rhoipteleaceae, and Casuarinaceae are dominated in the present day by forms with winged or very small fruits or seeds adapted for wind dispersal. The Hamamelidaceae have a few taxa that are wind dispersed, but the majority are ballistically dispersed. Where the above families are known in the fossil record, they are abiotically dispersed.

SUMMARY OF INTERMEDIATE FAMILIES

The Cannabaceae and Myricaceae possess fruits that are often enveloped in bracteoles. The fruits could float or be wind dispersed. The often spiny *Comptonia* bracteoles might adhere to animals. The fruits of these groups could also be eaten and dispersed. The fruit of the Leitneriaceae could equally well attract animal dispersers or float. The fossil records of the Cannabaceae, Myricaceae, and Leitneriaceae indicate no change in morphology of the fruit in the recorded past. The Ulmaceae possess approximately 25% abiotically-dispersed, and 75% animal-dispersed, species. The fossil record indicates that both dispersal modes appeared simultaneously, but that animal dispersal may have become more important during the Tertiary. Two-thirds of the species of the Urticaceae are abiotically dispersed, whereas 30% are animal dispersed. The fossil record of urticaceous fruits does not clearly indicate the nature of dispersal in the past. In the extant Juglandaceae, 63% of the species are biotically dispersed and 37% are abiotically dispersed. Senonian fruits of juglandalean affinity

are probably abiotically dispersed. Whereas both wind- and animal-dispersed fruits are present in the early Tertiary, there is a clear rise in dominance of biotically-dispersed species through the Tertiary (Fig. 9). Three genera of extant Betulaceae are wind dispersed, two can be wind or animal dispersed, and *Corylus* is animal dispersed. Abiotically- and biotically-dispersed betulaceous diaspores appear simultaneously in the fossil record.

SUMMARY OF BIOTICALLY-DISPERSED FAMILIES

The Daphniphyllaceae, Didymelaceae, and Balanopaceae possess fleshy fruits suggestive of animal dispersal; they all lack fossil records. The Moraceae are almost entirely animal dispersed today. The fossil record is possibly equivocal but could be read to show no evidence of abiotic dispersal. The Cecropiaceae are entirely biotically dispersed today and lack a fossil record. The Fagaceae are almost, if not entirely, biotically dispersed in the present day. Possible middle Late Cretaceous fagaceous fruits are abiotically dispersed. The next genus to appear in the fossil record of the family (*Fagopsis*) is wind dispersed. All others are animal dispersed.

DISCUSSION

BIOTIC DISPERSAL AND PHYLOGENY

At the outset, I outlined two assumptions; that the Hamamelidae reached a zenith in the Cretaceous and are largely a relict group today, and that abiotic dispersal is primitive in angiosperms. Given these premises, logic suggests that families dominated by biotic dispersal and included in the Hamamelidae may be mis-allied with the sub-class.

Biotic dispersal is important in three orders of the Hamamelidae; the Urticales (Ulmaceae, Moraceae, Cecropiaceae, Urticaceae), the Juglandales (Juglandaceae and Balanopaceae), and Fagales (Fagaceae and a small portion of the Betulaceae). In addition, it dominates the Daphniphyllaceae and Didymelaceae. With the exception of the last two small "outliers," all of the groups mentioned lie among the "advanced" Hamamelidae, and questions have been raised about the proper placement of all of these groups.

The Urticales have been allied with the Malvales (Dilleniidae) rather than with the Hamamelidae (e.g., Thorne, 1973; Berg, 1977), a solution perhaps borne out by leaf architecture (Leo Hickey, pers. comm.). However, separate evidence suggests assignment to the Hamamelidae (Cronquist, 1981: 186). The Juglandales have long been a bone of phylogenetic contention, with alternative views allying them with the Hamamelidae or the Rosidae [near Anacardiaceae (Sapindales)]. The dominance of biotic dispersal in modern representatives of the family would appear to support features of leaf architecture (e.g., Hickey & Wolfe, 1975) in arguing for their Rosid affinity. Again, however, there is much evidence for their association with the Hamamelidae (Cronquist, 1981: 204–207). The Fagales are not generally contested as Hamamelids, although Hickey and Wolfe (1975) did note that the leaf architectural affinities of the order (excluding Balanopales and Betulales) were "uncertain." Of the smaller families in question, Hickey and Wolfe (1975) transferred the Didymelaceae to the Dilleniidae and Thorne (1976) referred it to the Euphorbiales (both paralleling its biotic dispersal), but Cronquist (1981) considered it most harmoniously placed in the Hamamelidae. The Daphniphyllaceae are another taxonomic football, alternating between placement in the Euphorbiaceae (Rosidae) and the Hamamelidae (see Cronquist, 1981), but without resolution. Here the biotic dispersal would join evidence for a euphorbian alliance.

In summary, dispersal evidence would appear to support arguments for exclusion of the Juglandales, Didymelaceae, Daphniphyllaceae, and several families of the Urticales from the Hamamelidae and raises questions about the association of the Fagales with the sub-class. However, acceptance of these conclusions based on modern dispersal modes assumes that the families in question have not altered their primary mode of dispersal over time. The diversification of important groups of modern dispersal agents in the early Tertiary indicates that plant lineages dating from the Late Cretaceous or Tertiary (e.g., Juglandaceae, Fagaceae, Urticaceae) may have passed through a period of intense selective pressure involving changing dispersal mechanisms (Tiffney, 1984).

EVIDENCE FOR ALTERATION OF DISPERSAL MODE WITHIN A FAMILY

Two, possibly three, examples in the fossil record and one from modern evidence suggest that the dominant mode of dispersal changed over

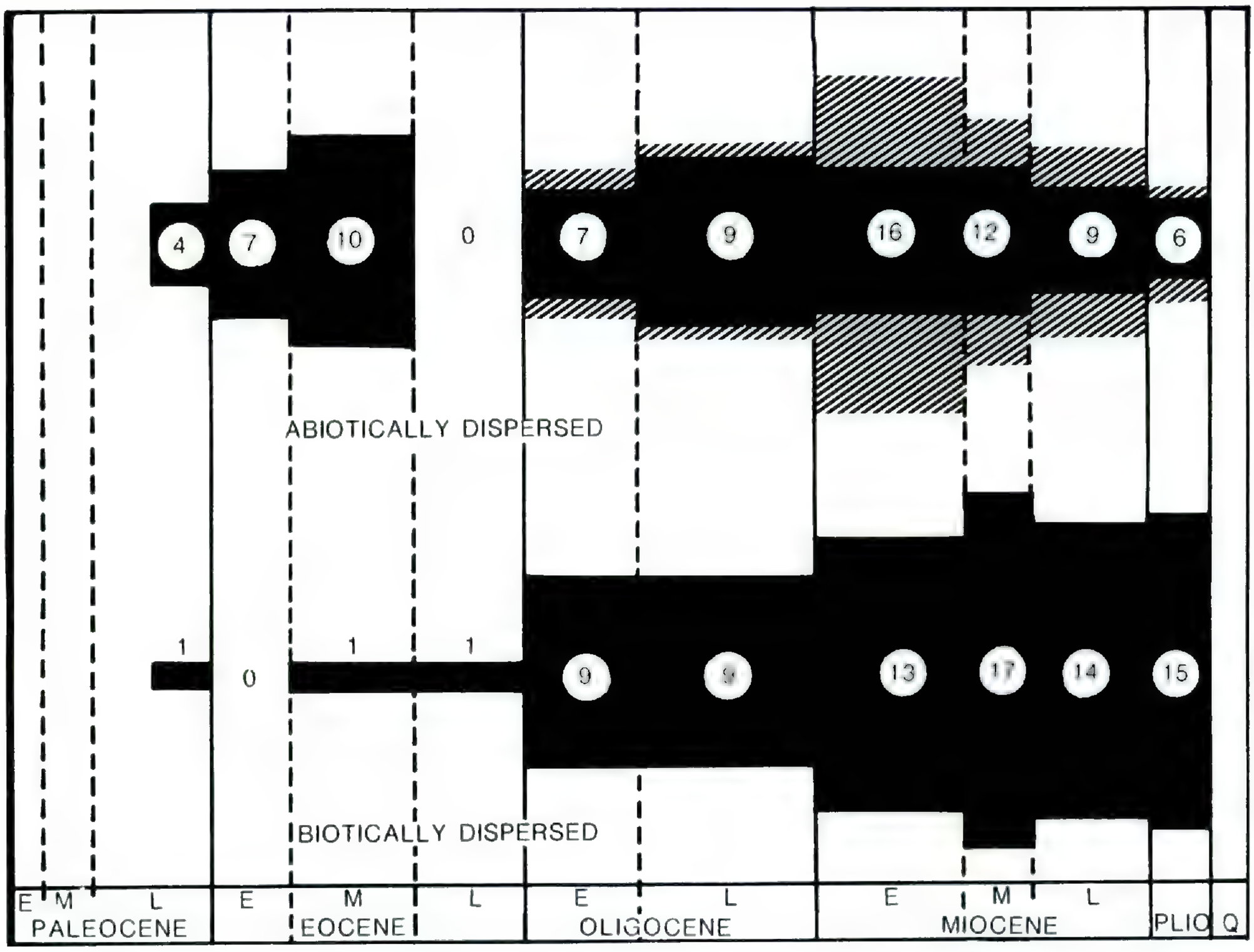

FIGURE 9. Specific diversity of abiotically-dispersed and biotically-dispersed Juglandaceae in the Tertiary. Data largely from Manchester (1981a); additional data from sources cited in Figure 6. Diagonally-lined area in upper spindle demonstrates the proportionately large contribution of *Pterocarya* to the diversity of abiotically-dispersed Juglandaceae in the later Tertiary. Numbers in each spindle indicate numbers of species present in each Epoch subdivision. Time convention as in Figure 1.

time within families. The fossil examples will be considered first and in order of increasing clarity.

Ulmaceae. The Ulmaceae is divided into the Ulmoideae (largely abiotically dispersed) and the Celtidoideae (largely biotically dispersed). Fruiting evidence of both subfamilies is recorded from the middle Paleocene (Fig. 3). Zavada and Crepet (1981) described flowers of Celtidoideae from the Middle Eocene of southeastern North America. In their discussion they noted that, in contrast to other Eocene fossil flowers of the "Amentifereae," which normally look modern at this time, these Celtidoid flowers were intermediate between insect-pollinated ancestors and the modern wind-pollinated flowers of the group. This conveys the impression that the Celtidoideae were still evolving in the mid-Eocene, and the hypothesis could be entertained that modern fruit and dispersal characters were also evolving in the group. However, such an interpretation ignores mosaic evolution and the likelihood that the evolutionary status of the flowers might have little to do with that of the fruits. Further, this interpretation presumes that the ulmoid flowers of the time were "modern," a conclusion for which no evidence exists. It is worth noting (Fig. 3) that, while two samaroid and two drupaceous genera are present in the Eocene, animal-dispersed forms have come to dominate the family by greater than a 2 : 1 margin. I suspect the Ulmaceae of having abiotic dispersal as the plesiomorphic state, but the actual evidence is very weak.

Fagaceae. Fagaceae are currently almost entirely animal dispersed. The Tertiary fossil record involves seven extant and two extinct genera. Of these, the extinct *Fagopsis* (Manchester & Crane, 1983) is both the earliest (Early Eocene through Late Oligocene) and is the only genus adapted to abiotic dispersal. The morphology of *Fagopsis* agrees with the cupules of other members of the family and argues for the derivation of structures for both biotic and abiotic dispersal from a common "cupule" morphology.

Late Cretaceous flowers from Massachusetts (Tiffney & Friis, unpubl. data) are similar to flow-

ers of extant Fagaceae, particularly those of *Lithocarpus*. The associated fruits are tiny, very numerous, and lack a cupule. Their great numbers and small size agree with Fey and Endress's (1983: 451) prediction that the origin of the cupule involved the reduction of the "highly branched system of modified (compact, sterile) ultimate parts of the inflorescential cyme." Such a reduction could also be linked to an increase in size of the remaining fruits, leading to the evolution of a single, large fruit. The tiny size and great numbers of these fruits argue for their abiotic dispersal.

The abiotic dispersal of the putative Cretaceous fagaceous fruits, together with the abiotic dispersal of the first clear fruit of the family to appear in the record, *Fagopsis*, suggests that the Fagaceae might be primitively abiotically dispersed. The rapid appearance of biotically-dispersed members of the family in the Tertiary could be seen as an adaptive response to the coeval radiations of mammals and birds.

Juglandaceae. Manchester (1981a; see also Manchester & Dilcher, 1982 and Wing & Hickey, 1984) has provided a detailed review of the history of the family with emphasis on its fruits. At the species level, abiotically-dispersed fruits dominated the early Tertiary record of the family; biotically-dispersed fruits diversified rapidly in the mid-Tertiary and dominate the family in the present day (Fig. 9). As found in the Fagaceae, this pattern is supported by Friis's (1983) data on three genera of fruits (*Manningia, Antiquocarya,* and *Caryanthus*) allied with the Juglandaceae in the Campanian. The mature fruits of all three are tiny and show no signs of fleshy parts leading one to assume abiotic dispersal.

This evidence suggests that the Juglandaceae (or the family and its immediate ancestors) were abiotically dispersed in the Late Cretaceous and earliest Tertiary. With the appearance of biotic dispersal agents, the family experimented with mechanisms of both biotic and abiotic dispersal. Presumably selection acted for larger endosperm reserves and therefore seed size (Tiffney, 1984) in the early Tertiary. This led to the simultaneous evolution of large-nutted, biotically-dispersed, fruits (*Juglans*) and the evolution of larger abiotically-dispersed fruits borne on increasingly larger winged structures (e.g., *Cyclocarya, Engelhardtia*). The forms with animal-dispersed fruits ultimately dominated the family. Of the wind-dispersed forms, only *Pterocarya* was successful in the later Tertiary, perhaps because of its small fruit and wing size; in the only reference to its site ecology, Wang (1961: 91) remarked that *Pterocarya stenoptera* C. DC. occurs "in small patches of pure communities in forest openings" implying that it is an early to mid-successional tree. This ecology is in keeping with the presumed early successional status (Tiffney, 1984) of the Late Cretaceous and Early Tertiary abiotically-dispersed members of the family.

Moraceae, Cecropiaceae, Urticaceae. Turning from the fossil record, there is evidence from the morphology of the Moraceae, Cecropiaceae, and to a degree, Urticaceae, that suggests these families underwent a transition from dominant abiotic to dominant biotic dispersal in their history. The Cecropiaceae are entirely animal dispersed today. In the extant Moraceae, 78% of the genera and 86% of the species are animal dispersed. The Urticaceae are mixed, with 47.6% of the genera and 29.3% of the species biotically dispersed. The common fruit morphology in all three families is an achene, or if the fruit wall is fleshy, a drupe. However, drupes occur in only 11% of the genera and 3% of the species in the Moraceae, only portions of one genus (*Coussapoa* Aubl.) of 50 species in the Cecropiaceae (20.7% of total number of species in the family), and only 4.3% of the genera and 1.3% of the species in the Urticaceae. Animal dispersal based on adherent fruits (sticky, hairy, or hooked) accounts for no more than 6% of the genera and 0.3% of the species of Moraceae and 13% of the genera and 12.8% of the species of Urticaceae. In all three families, the dominant structure associated with attracting animal dispersal agents involves either fleshy, accrescent calyx parts or an inflated, fleshy, receptacle. Both structures form succulent and attractively-colored berry mimics, but without the participation of the fruit wall; the fruit remains an achene buried in the externally-derived flesh. Many reports attest to the success of these "pseudo-drupes" in attracting birds or mammals [e.g., *Cudrania* Trécul, *Artocarpus* Forst., *Sloetia* Teij. & Binn. (*Streblus* Lour., see Ridley, 1930)]. Such "fruits" made of fleshy floral parts account for 67% of the genera and 82.8% of the species of Moraceae, 87.5% of the genera and 79.3% of the species of Cecropiaceae, and 30.3% of the genera and 15.2% of the species of Urticaceae. In some cases the floral parts aid in biotic dispersal by forming hairs or spines that stick to dispersal agents [e.g., *Rousselia* Gaudich. and *Soleirolia* Gaudich. (Urticaceae)]. Abiotic dispersal in all three families in-

volves both structures associated only with the achene and structures associated with the floral parts. In some genera [e.g., *Metatrophis* F. Brown (Moraceae), *Hemistylus* Benth. (Urticaceae)] the floral parts form wings, whereas in others [e.g., species of *Streblus* Lour., *Dorstenia* L. (Moraceae), *Pilea* Lindl., *Procris* Comm. ex Juss. (Urticaceae)] the calyx exerts pressure on the mature achenes and forces the fruits out of their floral envelope with great force (Ridley, 1930). Ballistic dispersal occurs in roughly 2% of the genera and 13% of the species of Moraceae, none of the Cecropiaceae, and 19.5% of the genera and perhaps as much as 58% of the species of Urticaceae.

The plesiomorphic status of the achene in this group is suggested but not proven by its wide distribution in all three families. It is also suggested by the fossil record, because the oldest fruiting remains of this group of families are achenes from the Late Cretaceous (Knobloch, 1971; Knobloch & Mai, 1984).

If abiotic mechanisms of dispersal dominated in the Cretaceous, and if the Urticaceae extend back to the Late Cretaceous, then it is possible that the dry and ballistically-dispersed achenes of the present day reflect the ancestral dispersal mechanisms of the Urticaceae, and by inference, the Moraceae and Cecropiaceae. If so, this implies that these families met the selective pressures of the evolving mammals and birds of the early Tertiary in two ways. The first was the evolution (once, or repeatedly) of fleshy exocarps to form drupes. To judge from the present day, this solution was not widespread. The second response was to build upon the specialization of the perianth, presumably already evolved for abiotic ballistic dispersal. Again, this potentially could have evolved repeatedly in several lineages. The accrescent floral parts could become fleshy, mimicking a berry without a topological re-arrangement of mature flower and fruit, or the developmental switch from a hard exocarp to a fleshy one underlain by a hard meso- or endocarp. This explanation is consistent with the important role that flower parts play in abiotic dispersal in the extant Urticaceae and to a lesser degree, Moraceae. It is also consistent with the perianth and receptacle-derived pseudo-berries that seem to form an important adaptive solution common to all three families. Tangentially, the early fossil record and the dominant abiotic dispersal mode of the Urticaceae suggests that they retain the greatest amount of plesiomorphic fruiting characters among the Cecropiaceae, Moraceae, and Urticaceae. This could be related to their herbaceous growth habit. In either case, the ecological nature of the Urticaceae is consistent with the proposed abiotic dispersal ecology of the Cretaceous angiosperms (Tiffney, 1984).

SUMMARY

The fossil record of the Juglandaceae and its immediate predecessors strongly suggests a transition from abiotic to biotic dispersal within the family. The fossil evidence for the Fagaceae is less strong, but also suggestive of such a transition. Evidence for a similar transition in the Ulmaceae is inferential, but again suggestive. The dominance of perianth-derived pseudo-fruits in the Moraceae and Cecropiaceae and their presence in the Urticaceae, the commonality of the achene morphology to all three families, and the mechanisms of abiotic achene dispersal in the Urticaceae, may be hypothesized to reflect an early Tertiary transition from abiotic to biotic dispersal in the Moraceae and Cecropiaceae, and the retention of more plesiomorphic characters in the Urticaceae.

Evolutionary Conclusions

RELATIONSHIP OF DIVERSITY AND DISPERSAL MECHANISMS

The distribution of generic and specific diversities in the Hamamelidae presents an interesting pattern (Fig. 10). Sixteen families have three genera or less, and 14 have only one genus. Only three of these families have more than ten species (Daphniphyllaceae—35 spp., Casuarinaceae—50 spp., Myricaceae—50 spp.). Four families have an intermediate diversity; the Juglandaceae with 9/60 (genera/species), the Hamamelidaceae with 28/100 plus, the Betulaceae with 6/120, and the Ulmaceae with 18/150. Four families have high diversities: Cecropiaceae (8/275), Fagaceae (8/800), Urticaceae (46/1,255), and Moraceae (51/1,313).

It is commonly assumed that insect pollination is a primary cause of the present diversity of angiosperms. However, biotic dispersal of fruits and seeds offers a similar potential for animal-mediated diversification. The Hamamelidae provide a natural experiment to demonstrate the effect of biotic dispersal on diversity. With rare exceptions, the included families are dominated by anemophily (the Hamamelidaceae is primarily insect pollinated, and a few species in the

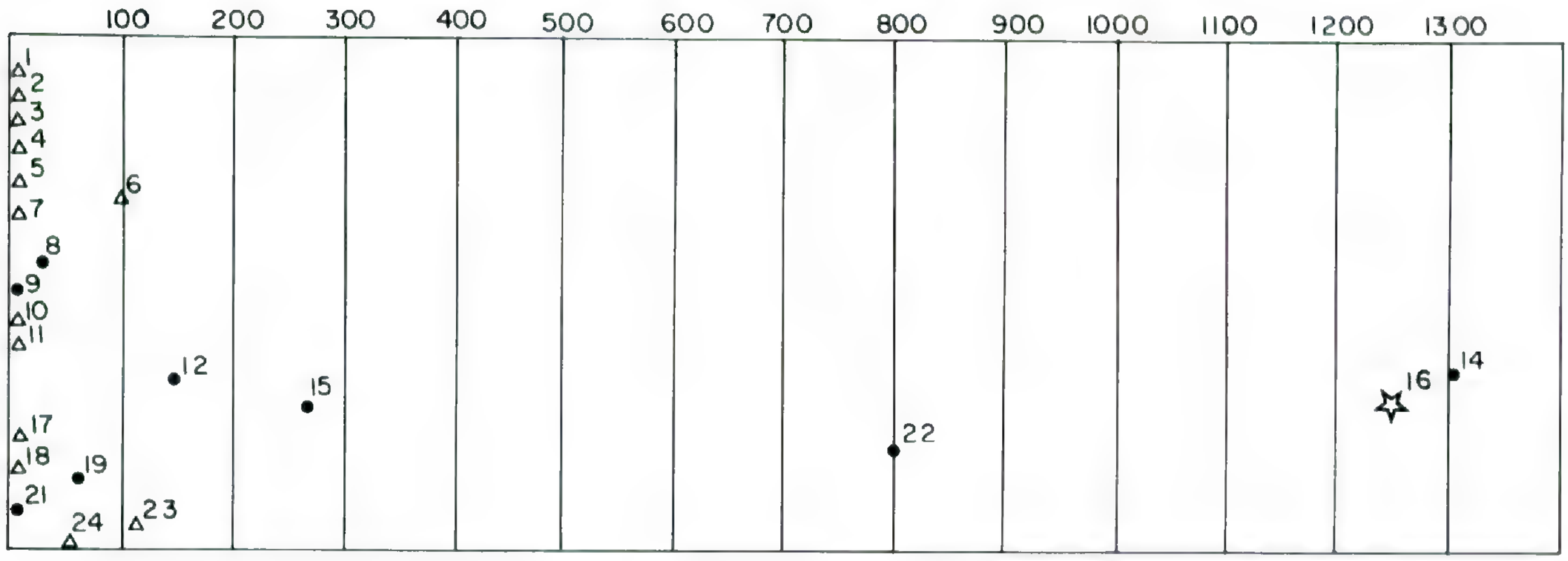

FIGURE 10. Plot of number of species per family for families in the Hamamelidae sensu Cronquist (1981). Points for Cannabaceae and Myricaceae omitted in light of absence of clear-cut dominant mode of dispersal. Horizontal axis, number of species; Vertical axis, valueless; Open triangles, families dominated by abiotic dispersal; Closed circles, families dominated by biotic dispersal; Open star, Urticaceae. Family identity indicated by the number by each symbol; the numbers corresponding to the order of families in Table 1.

Moraceae, Urticaceae, and Cecropiaceae are entomophilous, but these are unusual; similarly, the Fagaceae includes a few species that are secondarily entomophilous). In effect, the variable of insect pollination is controlled in the group. The only other variable that might confuse the proposed comparison is that of habit, however all the hamamelid families are dominantly (if not entirely) woody, with the exception of the Urticaceae, which are dominantly herbaceous.

Of the four families with substantially more than 150 species, only Urticaceae is not dominated by biotic dispersal. This anomaly may be explained largely by the herbaceous habit and shorter life cycle of most members of the latter family. Of the intermediate-sized families, Ulmaceae are dominated by biotic dispersal, Juglandaceae are dominated 2:1 by biotic dispersal, and Betulaceae possess both dispersal modes in unclear proportions. The Hamamelidaceae are abiotically dispersed, but their diversity could be explained by the dominant entomophily of the family. The small-sized families (50 species or less) are dominated (ten to four) by abiotic dispersal. A regression of species number per family against dispersal type (excluding data from the "generalized" Cannabaceae and Myricaceae) yields $r = 0.225$, below the 80% confidence limit. Elimination of the Urticaceae from the data set yields $r = 0.423$, which falls in the 90–95% confidence limit. Elimination of the Hamamelidaceae from consideration accentuates this effect. This pattern suggests the potential stimulating effect of biotic dispersal on the diversification of the angiosperms. The great diversity of the modern flora may be in large part a function of plant-animal interactions involving biotic diaspore dispersal, as well as the more frequently cited coevolution of angiosperms with pollinators and herbivores.

DISPERSAL PLASTICITY

Several examples demonstrate that dispersal mode changes within a family over time. Dispersal modes appear stable within genera, but this is an artifact: one would not identify an isolated fossil fruit as a modern genus unless it had the morphology of that genus. The demonstration of this plasticity is important on three counts. First, the appearance of animal-dispersed fruits within five to 15 million years after the radiation of mammals and birds in the early Tertiary is a measure of the reality of the concept of "coevolution" in a loose sense (cf. Herrera, 1985) and its significance in angiosperm evolution. Second, the response of fruit and seed morphology to the appearance of new dispersal agents further supports the importance of mosaicism in angiosperm evolution. For example, pollen data (Muller, 1981) suggest an earlier time of first appearance for many families than does that for fruits and seeds (Tiffney, unpubl. data). This suggests the separation of selective effects of pollinators and fruit/seed dispersers. Third, the flexibility of dispersal mechanisms over time within a family emphasizes the need to seek important phylogenetic characters of fruits and seeds in the

details of cell structure, cell layer sequence, etc., rather than simply in gross morphology.

EVALUATION OF HYPOTHESES

Two assumptions were made at the outset of this paper: (1) that the Hamamelidae originated and achieved their zenith in the Cretaceous, and (2) that Cretaceous angiosperms were largely abiotically dispersed and that biotic dispersal became important only in the early Tertiary. It is not possible to evaluate the first assumption from the fossil fruit and seed record, although fruiting material of some families (Platanaceae, Juglandaceae, possibly Urticaceae, and Fagaceae) is known from the Cretaceous. The second assumption (discussed by Tiffney, 1984) is supported by the apparent primitive status of abiotic dispersal demonstrated here for the Juglandaceae and possibly Fagaceae, and inferred for the Ulmaceae and possibly Moraceae, Cecropiaceae, and Urticaceae.

Given these assumptions, I predicted that (1) the majority of families in the Hamamelidae should have abiotic dispersal syndromes, and (2) that dispersal mode might provide an additional trait on which to assess the phylogenetic affinities of families whose alliance with the Hamamelidae has been questioned on other grounds.

The majority of families associated with the Hamamelidae in the scheme of Cronquist (1981) are abiotically dispersed (Table 1; 13 abiotic, seven biotic, and four either with roughly equal proportions of biotic and abiotic, or with generalized morphology and dispersal mechanism). However, evidence from the fossil record suggests that the Juglandaceae and perhaps Fagaceae underwent a transition from a dominantly abiotic mode of dispersal to a biotic mode in the early Tertiary; more circumstantial evidence suggests that the same might be true of the Ulmaceae and the Urticaceae and associated Moraceae and Cecropiaceae.

If the dominant mode of dispersal within a family can change over time, then the present dispersal characteristics are not an accurate guide of the past. The primitive dispersal state, while inferable from neontological evidence, can be demonstrated only through the fossil record. Thus, only in the case of the Juglandaceae, and perhaps of the Fagaceae, can we state that the primitive mode of dispersal was abiotic and that the dispersal mode does not contest the affinities of the family with the Hamamelidae. A similar transition from abiotic to biotic dispersal is suggested for the Ulmaceae by the fossil record, and for the Moraceae, Urticaceae, and Cecropiaceae by circumstantial morphological evidence; based on dispersal, the affinities of these families with the Hamamelidae cannot be evaluated. No fossil record exists for the Daphniphyllaceae, Didymelaceae, or Balanopaceae, thus there is no way to evaluate whether the biotic dispersal mechanisms of these taxa are primitive or derived.

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PHYTOCHEMICAL ASPECTS OF PHYLOGENY IN HAMAMELIDAE[1]

DAVID E. GIANNASI[2]

ABSTRACT

Chemical data for the Hamamelidae (sensu Cronquist) are numerous but scattered. Few large-scale comprehensive surveys of any particular group of compounds (micro- or macromolecular) exist for the Hamamelidae. This has limited the use of such data in drawing broad systematic conclusions beyond those based on extant morphological, anatomical, and palynological studies. Certainly, available data for some classes of compounds, such as phenolics, have proven useful at the inter- and intrafamilial level (e.g., Ulmaceae, Juglandaceae, Urticaceae). However, the diverse and sometimes "exotic" micromolecules (e.g., alkaloids, sesquiterpene lactones, polyacetylenes, glucosinolates) often found in the other subclasses of angiosperms are mostly lacking in the Hamamelidae. This implies, at least from present surveys, a biochemical conservatism (or alternatively, reduction) for the group and an early and considerable divergence from its more chemically diverse putative Magnoliid ancestors.

In an earlier review of the phytochemistry of the "Amentiferae," Mears (1973) catalogued the various classes of secondary metabolites for the group, including phenolics, sugars, various types of terpenoids (including iridoids), several alkaloids, and fatty acids. His major conclusions were that (1) insufficient comprehensive surveys of any class of secondary metabolites were available and thus (2) few correlations or putative relationships between taxa in the "Amentiferae" could be drawn.

More than ten years later (using computer-assisted and manual literature surveys), basically the same conclusions may be drawn despite a moderate increase in the number of new compounds discovered and an equally moderate increase in the number of families surveyed in detail for any single class of compounds (mostly phenolics). This is surprising for a group that has undergone considerable taxonomic redefinition and reemerged as the Hamamelidae (sensu Cronquist, 1981). Further, many of the reports are isolated identifications (single species, a few compounds) and with few exceptions (Venkataraman, 1972), little attempt has been made to summarize these scattered data. Most recent chemotaxonomic discussions of the Hamamelidae have been placed within the broader context of angiosperm phylogeny in general (e.g., Gershenzon & Mabry, 1983; Gornall et al., 1979; Harborne, 1977; Harborne et al., 1975; Harborne & Mabry, 1982; Young, 1981; Young & Seigler, 1981).

To be sure, several families have been surveyed in detail, such as the Betulaceae (Wollenweber, 1975) and Ulmaceae (Giannasi, 1978), as have several genera, for example, *Fagus* (Giannasi & Niklas, 1981) with, in some cases, emphasis on different tissues such as wood chemistry, for example, Moraceae (Venkataraman, 1972). All have been helpful at their respective taxonomic levels but of limited use above the family level. Macromolecular data for the Hamamelidae, in the form of serological studies, are now available through the efforts of Fairbrothers and co-workers (Brunner & Fairbrothers, 1979; Petersen & Fairbrothers, 1979, 1983, 1985). However, many of the phytochemical correlations that do exist for the Hamamelidae still rest on earlier secondary metabolite surveys, primarily phenolics, and it is here that major emphasis continues (Egger & Reznik, 1961; Bate-Smith, 1962; Kubitzki & Reznik, 1966; Jay, 1968).

This discussion is intended to: (1) provide a summarized update of the earlier review by Mears (1973) in terms of some of the new classes of compounds discovered in the Hamamelidae in the past ten years and (2) to highlight several types of chemical data that have recently been

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TABLE 1. Subclass Hamamelidae according to Cronquist (1981).

Subclass Hamamelidae	Putative Relationships or Alternative Treatments[a]
Trochodendrales	Magnoliidae
Tetracentraceae	Hamamelidaceae; *Altingia, Liquidambar*
Trochodendraceae	
Hamamelidales	Trochodendrales
Cercidiphyllaceae	Hamamelidaceae (*Disanthus*)
Eupteleaceae	Cercidiphyllaceae, Platanaceae, Magnoliidae (Schisandraceae)
Platanaceae	
Hamamelidaceae	
Myrothamnaceae	
Daphniphyllales	
Daphniphyllaceae	Euphorbiaceae
Didymelales	—
Didymelaceae	Leitneriaceae, Euphorbiales, Thymelaceae
Eucommiales	
Eucommiaceae	Urticales, Hamamelidaceae, Magnoliales
Urticales	Malvales
Barbeyaceae	Malvales
Ulmaceae	Fagaceae, Betulaceae
Cannabaceae	Moraceae
Moraceae	
Cecropiaceae	Moraceae, Urticaceae
Urticaceae	Moraceae
Leitneriales	
Leitneriaceae	Didymelales
Juglandales	Rutales (Sapindales)
Juglandaceae	Anacardiaceae (Julianaceae)
Rhoipteleaceae	Myricaceae, Fagaceae, Betulaceae
Myricales	Juglandales, Fagales
Myricaceae	
Fagales	
Balanopaceae	
Fagaceae	
Betulaceae	*Trigonobalanus*, Fagaceae
Casuarinales	
Casuarinaceae	Betulaceae, Myricaceae

[a] Taxa in this column represent alternative taxa in which the Hamamelidae (sensu Cronquist, 1981) have been placed by other authors (see text at right for references).

applied to systematic problems in the Hamamelidae, sensu Cronquist (1981). The latter Hamamelid concept is chosen primarily because of my personal familiarity with the system and its innate pedagogical convenience as a framework against which other treatments may be compared. It certainly has provided a focal point for the spirited systematic discussion over the definition of the Hamamelidae.

The historical development of the concept of the "Amentiferae" into the Hamamelidae has been described by Stern (1973). There are also several different treatments of the Hamamelidae (within larger angiosperm classifications) in contemporary systematics (Conquist, 1968, 1981; Thorne, 1983; Dahlgren, 1980; Takhtajan, 1954, 1969, 1980). Some of these undergo regular revisions (Dahlgren, 1977, 1980, 1983; Thorne, 1973, 1976, 1977, 1983). Others are more specific reviews of the Hamamelidae alone (Abbe, 1974; Endress, 1977; Meeuse, 1975) or of specific orders along with other putative relationships within the subclass (e.g., Berg, 1977). Merxmüller (1977) has succinctly commented on the relative merits of a number of these systems.

Depending on one's taxonomic predilection, the Hamamelidae contain the taxa shown in Table 1, the left-hand column of taxa representing Cronquist's treatment, the column to the right showing a selection of some other relationships suggested by other workers. Most authors concur that a basic "core" of taxa including the Hamamelidales and Fagales probably represent the true concept of Hamamelidae (and then perhaps conservatively only the type families). All the other orders (a number of which are monotypic or at least monogeneric) are moved with great frequency (and often with justifiable logic) to other subclasses, orders, or families and back again. The phytochemist is often at a loss as to which and how many taxa to sample to provide an adequate survey of what various taxonomists consider the Hamamelidae and related taxa.

CHEMICAL REVIEW

If any group has exploited the use of phenolic compounds, surely it is the Hamamelidae. Since many taxa in Hamamelidae are woody, or essentially so, this is perhaps not unexpected and Cronquist (1977) attributed this characteristic phenolic synthesis, especially tannins, to a general chemical adaptation to herbivore deterrence by these compounds. Also, many unusual phenolic compounds are found in various members of this subclass (Mears, 1973) as in, for example, the Moraceae (Fig. 1; cf. Venkataraman, 1972). However, as Mears indicated, many of these compounds often are characteristic of only a few

species or a genus or a family and thus of little taxonomic help beyond that taxonomic level, especially in confirming or denying their position in the Hamamelidae. Alternatively, these compounds may be scattered throughout other disparate taxa in the angiosperms as a whole. The current known distribution of flavonoid biflavonyls is an example of such a class of compounds. In other cases, probably the majority, comprehensive surveys are lacking. Any heady phylogenetic relationship among plant taxa based on the presence or absence of a single or limited number of chemical characters often lasts only until the publication of the next phytochemical survey.

In general, tannins, proanthocyanidins (e.g., prodelphinidin), ellagic acid, and especially myricetin (and other vicinyl-hydroxylated compounds), are common to the Hamamelidae (Fig. 1). They have been used most commonly to separate the Hamamelidae (generally present) from the Magnoliidae (generally absent), although there are reports of their scattered occurrence in the Rosidae and Dilleniidae as well, with single isolated reports in the Asteridae and Liliopsida (although the Nymphaeales commonly have both ellagic acid and myricetin). A few species of the Magnoliidae also possess myricetin (Piperales, Laurales). The flavonoids in the Hamamelidae, while produced in large quantities, are often qualitatively simple flavonols (myricetin, quercetin, kaempferol). Some taxa possess glycoflavones, but with flavones generally low in number, at least by present survey data. O-methylation of flavonols and flavones in the Hamamelidae also seems to be low, with some exceptions (Betulaceae, Wollenweber, 1975; Moraceae, Venkataraman, 1972), but certainly not to the extent seen in other subclasses (e.g., Rosidae, Dilleniidae, Asteridae). Thus, the Hamamelidae possess a qualitatively conservative flavonoid complement, again at least by present surveys—perhaps the most significant caveat for such conclusions.

The occurrence of biflavonyls (Fig. 1) in *Casuarina* is unusual, as is their occurrence in a few other angiosperms. These flavonoid dimers are more consistently characteristic of gymnosperms and some lower tracheophytes (except ferns) and a moss or two. In angiosperms they occur in such disparate groups as Nandinaceae (Ranunculidae), Rhamnaceae, Euphorbiaceae, Thymelaceae, Ochnaceae, Clusiaceae (Guttiferae), Anacardiaceae, Burseraceae, Caprifoliaceae, and most recently have been found in the monocots, the Amaryllidaceae (Liliaceae). Their scattered distribution offers little systematic value at this time and may represent isolated parallel synthetic capabilities or perhaps only a lack of comprehensive surveys (Geiger & Quinn, 1975, 1982). More typical flavonoid monomers also occur commonly in *Casuarina* spp. consisting of a number of glycosidic variations based on a conservative aglycone complement of myricetin, quercetin, and kaempferol (Saleh & El-Lakany, 1979).

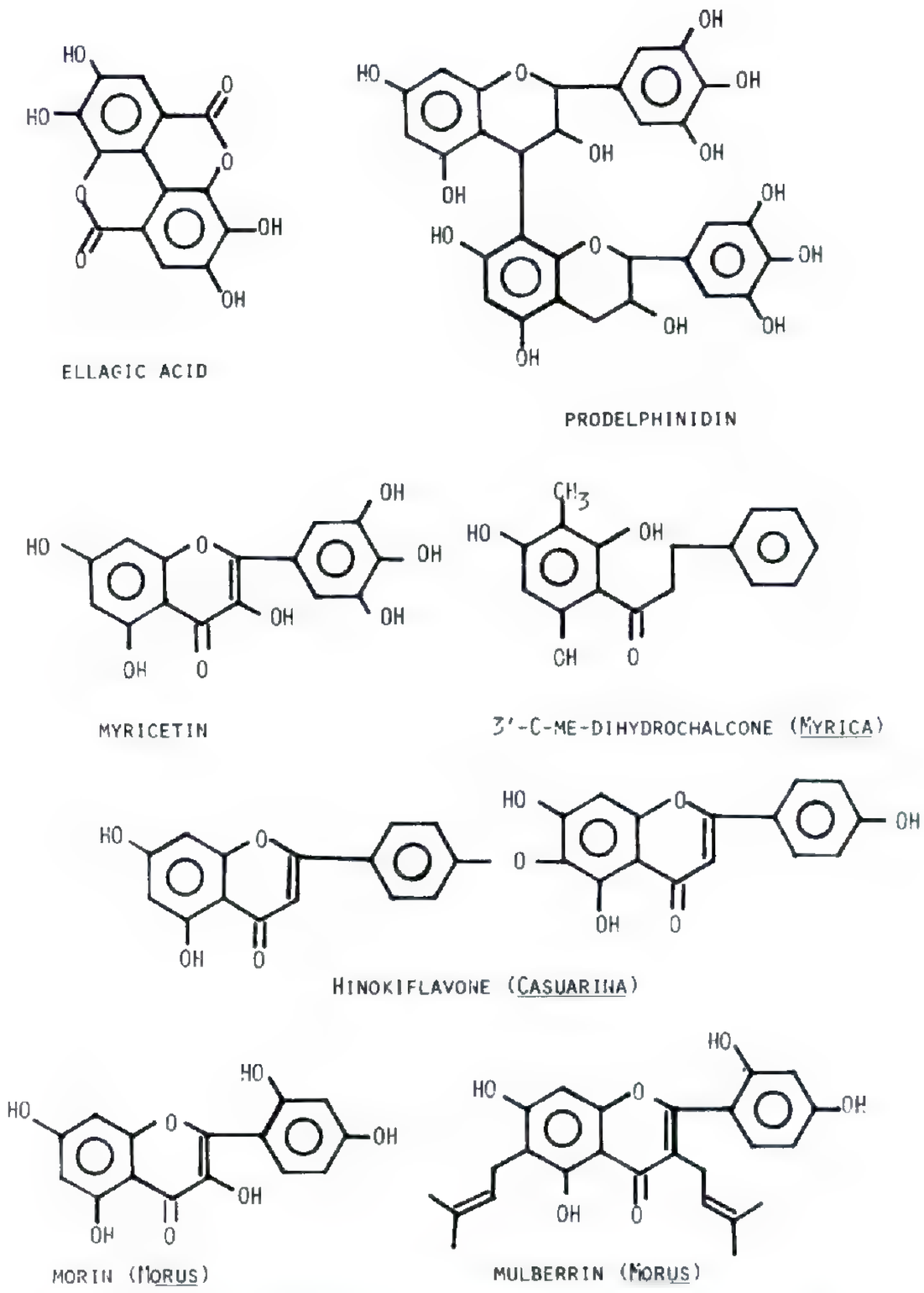
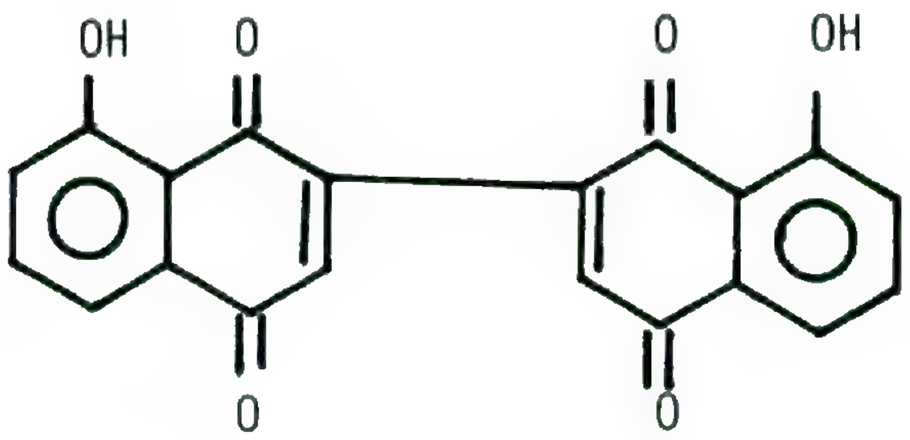


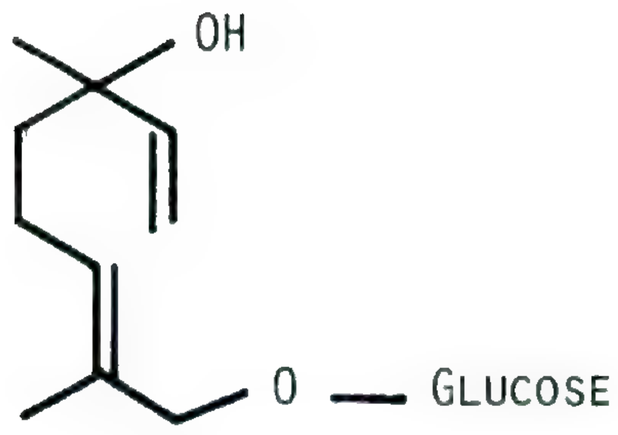
FIGURE 1. Examples of different types of phenolics in the Hamamelidae.

Quinones (Fig. 2) are found in several families in the Hamamelidae, especially the Juglandaceae, which produces the allelopathic agent, juglone, and several allied compounds such as bis-juglone (Gupta et al., 1972; Pardhasaradhi & Babu, 1978). Mixed phenolic-terpene (and sesquiterpene) quinones such as the aromatic naphthalenes of Ulmaceae heartwoods are known (Mears, 1973) along with some rare flavonol and flavanonol C-glycosides (Thomson, 1979; Hillis & Horne, 1966) and unusual C-methyl dihydrochalcones in *Myrica* (Malterud et al., 1977; Uyar et al., 1978). Fatty acid patterns in nut oils of *Carya* species have also been employed with systematic success (Stone et al., 1969).



3, 3'-BISJUGLONE

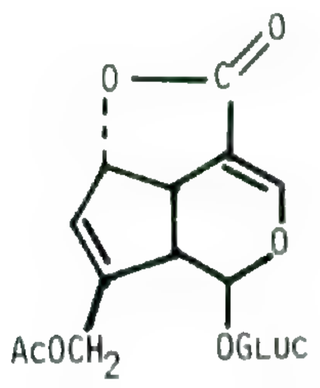
JUGLANS REGIA



LINOOL-9-O-GLUCOSIDE

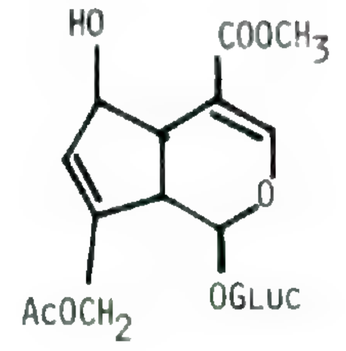
BETULA ALBA

FIGURE 2. Quinone and monoterpene types in the Hamamelidae.



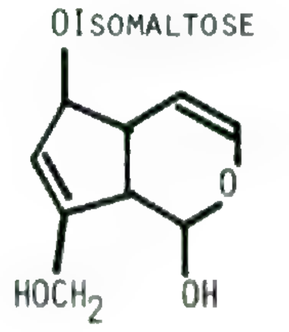
ASPERULOSIDE

DAPHNIPHYLLACEAE



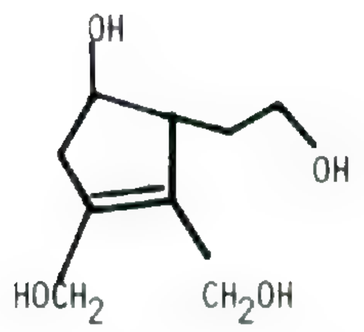
DAPHNIPHYLLOSIDE

DAPHNIPHYLLACEAE



ULMOSIDE

EUCOMMIACEAE



EUCOMMIOL

EUCOMMIACEAE

FIGURE 3. Examples of iridoids found in some Hamamelidae.

Several types of terpenes are found in the Hamamelidae. Typical monoterpenes are found in *Myrica* (Myricaceae) and these have been used for chemosystematic purposes (Halim & Collins, 1973). Unusual monoterpene glycosides (Fig. 2) occur in *Betula* (Tschesche et al., 1977). Monoterpene lactones or iridoids (Fig. 3) have also been found in the Hamamelidaceae (*Liquidambar*), Daphniphyllaceae (*Daphniphyllum*), Eucommiaceae (*Eucommia*), and Didymelaceae (*Didymeles*). Undoubtedly more will be discovered as specific surveys continue (El-Naggar & Beal, 1980; Kaplan & Gottlieb, 1982; Gershenzon & Mabry, 1983; Bianco et al., 1982). At this time the presence of iridoids in a few Hamamelidae further isolates this group from the Magnoliidae, which currently appear to lack them. Sesquiterpene lactones appear to be absent from the Hamamelidae as well but present in the Magnoliidae, providing yet another distinguishing character between the two subclasses.

In terms of nitrogen containing secondary products, glucosinolates appear to be absent from all Hamamelidae regardless of whose taxonomic scheme is used. Reports of cyanogenic glycosides (Fig. 7) rest mainly on color tests rather than extensive specific compound identifications. Such color tests have been reported for several families (Hamamelidaceae, Fagaceae, Juglandaceae). Complete identification is needed to clear this up especially in a biosynthetic sense (Hegnauer, 1973, 1977), but the few found are of the tyrosine-derived types.

Several types of alkaloids occur in the Hamamelidae (Fig. 4). Most are characteristic of a genus or two and of limited use due to their restricted occurrence, inadequate survey, or scattered occurrence in seemingly unrelated (at least not closely related) taxa (Mears, 1973). These include tropine types (pseudopelletierine) in *Ficus* (Moraceae) along with the tylophoric alkaloids, which also occur in *Tylophora* (Asclepiadaceae) and *Cryptocarya* (Lauraceae). A series of diterpene alkaloids (e.g., daphniphylline, daphnigraciline) have been reported from *Daphniphyllum gracile*, mostly from bark, and as yet are

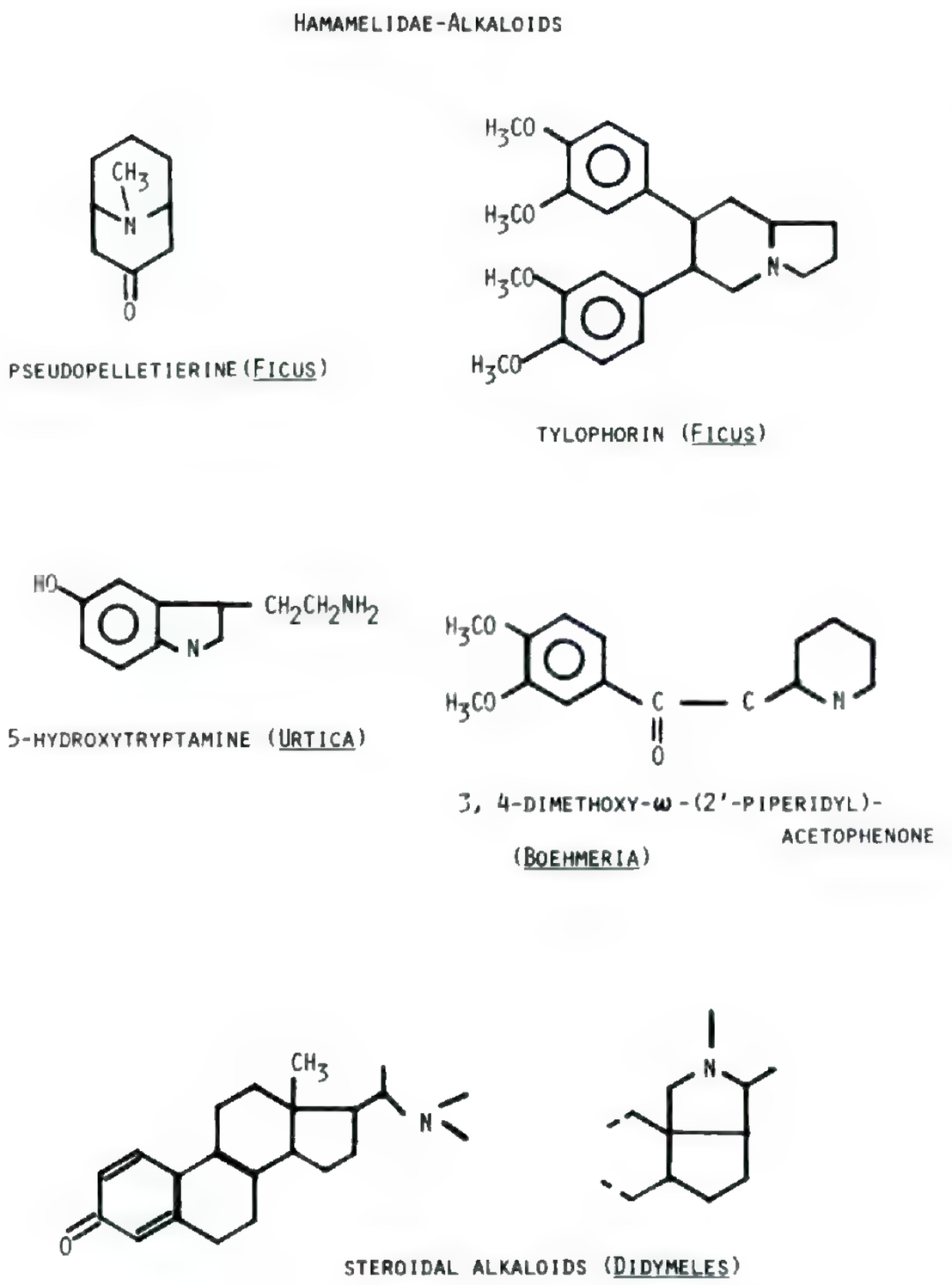


FIGURE 4. Alkaloids in the Hamamelidae.

taxonomically isolated in this occurrence (Grundon, 1977, 1981; Yamura et al., 1977, 1980). Steroid alkaloids have also been discovered in *Didymeles* (Ahond et al., 1980). The Hamamelidae generally appear to lack the tyrosine/phenylalanine-derived (benzyl-) isoquinoline alkaloids of the Magnoliidae-Caryophyllidae-Lilliidae (Liliopsida). In this way, the Hamamelidae are more like Rosidae-Dilleniidae-Asteridae, in which non-aromatic derived alkaloids (amino acids from TCA cycle or terpenoids) begin to predominate.

Obviously there is an unusual variety of secondary metabolites in the Hamamelidae, but comprehensive surveys are lacking. The few chemical studies of specific genera or families using single classes of compounds in detailed surveys have produced both interesting systematic results and grist for the chemist's mill, as indicated in the following discussion.

CHEMOSYSTEMATIC STUDIES—MICROMOLECULAR

Some of the more recent comprehensive studies in the Hamamelidae have centered on the Ulmaceae. An early flavonoid study of *Ulmus* and several related genera (Bate-Smith & Richens, 1973) showed that flavonoid evolution in the genus probably proceeded by reduction in flavonoid types and content (mostly flavonols). Bate-Smith and Richens also noted that several other related genera differed in their possession of flavone compounds but did not pursue it further. Subsequent studies by Giannasi and Niklas (1977) suggested that a flavonoid dichotomy existed between *Ulmus* (flavonols) and *Celtis* (glycoflavones). A comprehensive flavonoid aglycone study (Giannasi, 1978) confirmed this dichotomy as shown in Table 2. This generic arrangement generally matches that of Grudzinskaya (1965), who had previously proposed two separate families (Ulmaceae and Celtidaceae) rather than the more common treatment of two subfamilies (cf. Giannasi, 1978, for discussion and references). Later, SEM pollen analyses by Zavada supported Grudzinskaya's treatment (Zavada, 1983). As Zavada indicated, these data, along with fossil evidence (Zavada & Crepet, 1981), suggest that the two subfamilies have had a separate phylogenetic history since Eocene times and perhaps earlier.

TABLE 2. Generic distribution of flavonoids in the Ulmaceae (Giannasi, 1978).

	Flavonoids	Affinity[a]
Flavonols		
1.	*Ampelocera*	C
2.	*Aphananthe*	C
3.	*Barbeya*	(—)
4.	*Chaetoptelea*	(—)
5.	*Hemiptelea*	U
6.	*Holoptelea*[b]	U
7.	*Mirandaceltis*	(—)
8.	*Phyllostylon*	U
9.	*Planera*	U
10.	*Ulmus*	U
11.	*Zelkova*	U
12.	*Gironniera*: *Galumpita*[c]	
Glycoflavones		
12a.	*Gironniera*: *Gironniera*	C
13.	*Celtis*	C
14.	*Chaetachme*	C
15.	*Lozanella*	C
16.	*Parasponia*	C
17.	*Plagioceltis*	(—)
18.	*Pteroceltis*	C
19.	*Trema*	C

[a] According to Grudzinskaya (1965); C = Celtoid, U = Ulmoid, (—) = not considered by Grudzinskaya.
[b] Data from Bate-Smith and Richens (1973).
[c] Placed in *Aphananthe* by some authors.

TABLE 3. Leaf flavonoid[a] distribution in genera of the Juglandaceae (Giannasi & Niklas, unpubl. data).

Taxon[b]	Flavonols			Flavones	Glycoflavones	Flavanonols		Phenolics	
	M	Q	K	A	A	DQ	DK	EA	GA
Platycarya (1)		+	+	+		+		+	
Pterocarya (6)		+	+	+		+		+	
Alfaroa (3)		+	+	+		+		+	
Juglans A. (7)	+	+	+	+		+	+	+	+
B. (6)		+	+	+		+		+	+
Carya A. (6)	+	+	+	+		+		+	
B. (6)		+	+	+	?	+		+	
Oreomunnea A. (1)	+	+	+	+		+		+	
B. (1)		+	+	+		+			
Engelhardia (3)	+	+	+	+		+		+	

[a] Abbreviations: M = myricetin, Q = quercetin, K = kaempferol, A = apigenin, DQ = dihydroquercetin, DK = dihydrokaempferol, EA = ellagic acid, GA = gallic acid derivatives, + = present, ? = not completely confirmed.

[b] Number in parentheses indicates number of species examined in each genus.

The Juglandaceae are another recently studied group. Cronquist (1981) placed them in their own order along with the Rhoipteleaceae. Thorne (1983), however, placed the family in his superorder, Rutiflorae, suborder Juglandineae, not far from the Anacardiaceae (suborder Rutinae); Dahlgren (1980) places them in his Rosiflorae along with most of the Hamamelidae (sensu Cronquist, 1981).

In a recent flavonoid study of the Juglandaceae (Giannasi & Niklas, unpubl. data) it was found that mostly common flavonol glycosides, including those of myricetin, quercetin, and kaempferol along with two flavanols were produced in the leaves of the Juglandaceae (Table 3). Flavones and glycoflavones apparently are absent, or if present occur in trace amounts that are difficult to recover. The several genera examined may be separated into two major groups based on the presence or absence of myricetin glycosides, as shown in Table 3. All of the genera that produce myricetin occur in the New World. If the presence of myricetin is considered a primitive character, then one-character chemotaxonomy would suggest that the family may have originated in temperate North America. Indeed, the only exception to this is the Asian genus *Engelhardia,* which does produce myricetin. However, this apparently "Asian" taxon producing myricetin was widely represented in North America during Eocene times (Dilcher et al., 1976; Crepet et al., 1975), its current remaining Asian "endemism" being a secondarily derived or simply fortuitous relictual distribution. The myricetin marker compounds also proved to be useful in confirming the taxonomic affinities of a Miocene fossil leaf compression as that of a *Juglans* and its putative relationship to North American taxa.

The presence of this rather conservative leaf flavonoid complement in the Juglandaceae certainly allows the family to lie comfortably within the Hamamelidae. A suggested relationship of the Juglandaceae with or close to the Anacardiaceae, based primarily on the presence of ellagic acid and myricetin in both taxa, does not seem strong at this point, especially, when compared with the large number of unusual flavonoid types found in the Anacardiaceae (including Julianiaceae) by Young (1976, 1979). The Anacardiaceae, for example, possess anthochlor pigments, methylated flavonols, and 5- and 7-deoxyflavonoids not found in the Juglandaceae. Also, the lack of 5-methoxy flavonoids in the Anacardiaceae suggests that the Juglandaceae (which do possess them) are more compatibly retained in the Hamamelidae (at this time). The presence of biflavonyls in the Anacardiaceae absolutely sets this family apart from the Juglandaceae in which they are unknown.

A comprehensive survey of leaf bud flavonoid exudates has been carried out on the Betulaceae, including the genera *Betula, Alnus,* and *Ostrya* by Wollenweber (1975). All three genera could be distinguished on the basis of their flavonoids, and considerable interspecific flavonoid differences were observed within each genus. What was most interesting was the very large number of O-methylated flavonols that occurred in these genera, as well as a few methylated flavones, a flavonoid character of advancement (including

6-hydroxylation) observed only in some Rosidae and Asteridae, but not in other Fagales based on published surveys. Strangely enough, myricetin glycosides are not reported in the bud scales but commonly occur in the mature leaves along with several of the flavone and flavonol types cited for bud scales (Giannasi, unpubl. data). The family, therefore, seems to possess some advanced (or specialized) biosynthetic capability (O-methylation, 6-substitution) within the Hamamelidae, although more primitive myricetin glycosides do appear in the leaves of some species of *Betula*.

Beyond these few comprehensive surveys, most discussions are based on older broad surveys of aglycone hydrolysis in angiosperms (Bate-Smith, 1962; Lebreton, 1965; Jay, 1968) in which the flavonol aglycones are reported. A few (Kubitzki & Reznik, 1966; Gurni & Kubitzki, 1981; Egger & Reznik, 1961) do identify other flavonoids and their glycosides. Flavones or other compounds generally are not cited even though they are present (see below), which can give rise to spurious interpretations as we shall see.

Chemosystematic Studies—Macromolecular

Available macromolecular data on taxa in the Hamamelidae emanate from the efforts of Fairbrothers and colleagues (Brunner & Fairbrothers, 1979; Petersen & Fairbrothers, 1979, 1983) and have been obtained at several taxonomic levels.

In a serological study of the Corylaceae (Brunner & Fairbrothers, 1979), serological affinities of representative taxa from *Alnus, Betula, Carpinus, Corylus,* and *Ostrya* were examined. Using four serological techniques the genera could be divided into three major groups: (1) *Alnus,* (2) *Betula,* and (3) *Carpinus, Corylus,* and *Ostrya. Betula* proved to be the most serologically isolated taxon of the five but showed closest affinities with *Alnus. Alnus,* though distinct, was most similar to *Corylus* of Group 3. Overall similarities between all five genera suggest that they be retained within a single family (as tribes corresponding to the serological groupings) rather than elevating Group 3 to familial status, that is, Corylaceae.

In a second study (Peterson & Fairbrothers, 1979), an attempt was made to determine if the Juglandaceae, Myricaceae, and Fagaceae were closest to a Hamamelid origin (Cronquist, 1981; Takhtajan, 1969; Hutchinson, 1959) or if the Juglandaceae and Myricaceae are of a Rutalean origin near the Anacardiaceae (Thorne, 1976) with only the Fagaceae and Hamamelidaceae retained within the Hamamelidae, or one of several other possibilities mentioned by the other workers. Serology indicates that the Fagaceae and Myricaceae are closely related and show close similarity with the Juglandaceae as suggested by Cronquist (1981) and Takhtajan (1980). Little similarity between these three families and the Anacardiaceae was observed, thus failing to support such a relationship. As mentioned earlier, our own flavonoid surveys of the Juglandaceae also fail to support any strong relationship with the Anacardiaceae.

In a third study, an attempt was made to deal with one of the peripheral taxa in the Hamamelidae (sensu Cronquist, 1981), the Leitneriales, a monotypic order (Peterson & Fairbrothers, 1983) placed close to the Hamamelidales and near the Fagales-Myricales-Juglandales by Cronquist. In fact, serology suggests that the strongest affinity of the Leitneriales lies with *Ailanthus* and *Picrasma* of the Simaroubaceae and thus it is of Rutalean origin rather than of Hamamelid origin.

With the limited macromolecular data available, support is given in various examples for a broad concept of the Betulaceae, a solid relationship of Hamamelidales-Fagales-Myricales within, or as, the Hamamelidae (or at least as a natural taxonomic unit regardless of whose treatment is followed) and the removal of a peripheral group, Leitneriales, to the vicinity of the Simaroubaceae (Petersen & Fairbrothers, 1985). The results are encouraging and we can only hope that further studies will be conducted.

Hamamelidae—Current Surveys

I also undertook a limited survey of phenolics and flavonoids in the Hamamelidae both to check the results of earlier studies, especially the monumental work by Bate-Smith (1962) as well as others (Lebreton, 1965; Jay, 1968) and to add data for a few additional taxa where possible. The methodology employed was that of Giannasi (1978).

It was observed in the earlier studies that usually only the presence of flavonol aglycones was reported although from my own studies it was often obvious that other flavonoid classes were also present. My own studies further indicated that these other compounds were glycoflavones and flavones, in addition to the flavonols. Thus, the earlier studies, which emphasized only fla-

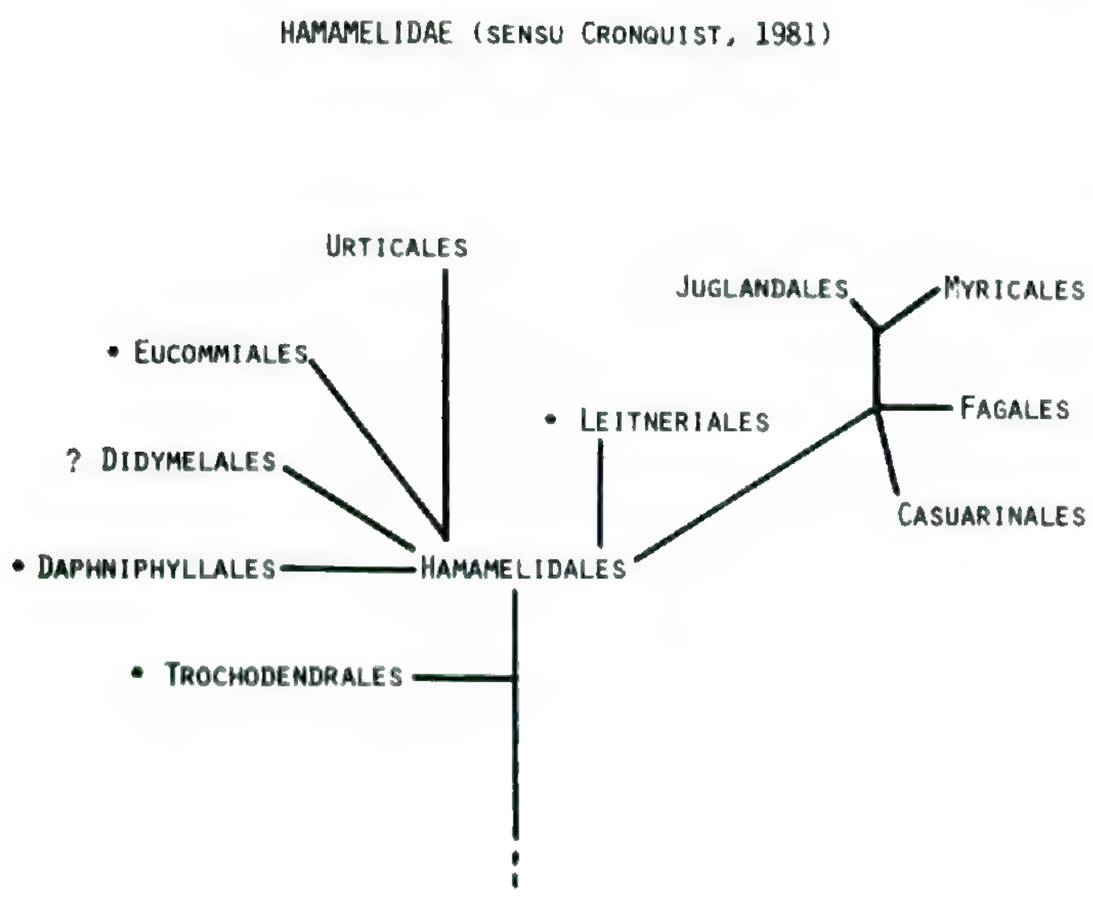


FIGURE 5. Putative phylogeny of the Hamamelidae (sensu Cronquist, 1981). Asterisk indicates lack of ellagic acid and myricetin compounds.

TABLE 4. Glycoflavone distribution in some Hamamelidae.

Family	Genera
Glycoflavones	
Cecropiaceae	*Cecropia, Pourouma*
Hamamelidaceae	*Sinowilsonia*
Moraceae	*Helicostylis, Ficus*
Urticaceae	*Urtica*(?)
Glycoflavones/Flavonols	
Hamamelidaceae	*Hamamelis*
Leitneriaceae	*Leitneria*(?)
Moraceae	*Helicostylus, Cudrania*
Glycoflavones/Simple Flavones	
Moraceae	*Ficus, Dorstenia, Broussonettia*
Glycoflavones/Flavones/Flavonols	
Cannabaceae	*Humulus*

vonols, inadvertently left out other flavonoids of considerable potential taxonomic importance, especially when comparing different subclasses, as we shall see below. In my own survey I was unable to confirm the presence of some aglycones cited in earlier studies of the same taxa. In some of these taxa I found additional aglycones not previously noted. In these cases such differences are most likely attributable to natural infraspecific variation exhibited by some taxa. The presence of flavonol aglycones (myricetin, quercetin, kaempferol) often depended on the number of collections sampled, sometimes requiring a composite flavonoid score from several or more collections to characterize a taxon. For example, in the extensive literature survey by Gornall et al. (1979) the Casuarinaceae were said to lack myricetin (Bate-Smith, 1962), but a contemporary detailed survey (Saleh & El-Lakany, 1979) as well as my own survey clearly document the presence of myricetin and the relative small quantities of biflavonyls produced in the leaves of *Casuarina* species. Therefore, all of these general surveys, including my own, that included taxa not sampled previously, must be considered provisional. Nevertheless, some correlations may suggest several phyletic trends in the evolution of the Hamamelidae and among its related subclasses.

If we consider Cronquist's phylogenetic treatment of the Hamamelidae (Fig. 5) we find that the "core" orders of the subclass possess myricetin and ellagic acid. A summarization of such data (Table 6) at the ordinal level suggests a "backbone" group consisting of the Hamamelidales-Fagales-Juglandales-Myricales-Casuarinales-Urticales. Similarly, many of the "peripheral" orders such as the Trochodendrales, Daphniphyllales, Eucommiales, and Leitneriales, whose presence in the Hamamelidae has been debated, lack both ellagic acid and myricetin, a fact confirmed by earlier and present studies. Care must be taken in using these generalizations, however, since not all species within a genus (e.g., *Myrica*) possess these characters although most do (Table 5), nor do all families within the "core" orders characterized by these constituents possess them (Table 6; e.g., Urticales, Hamamelidales). Indeed, in dealing with genera that may contain several hundred taxa, existing studies are certainly provisional.

Despite these caveats, several correlations and resultant hypotheses for the taxonomic grist mill are warranted based on current evidence. For example, the presence of myricetin and ellagic acid is considered a primitive chemical character (Bate-Smith, 1962; Harborne 1977). This also suggests that the peripheral orders of the Hamamelidae that *lack* these chemical characters may represent (1) a separate subclass, but closely related to the "core" Hamamelidae, and/or (2) a group of taxa exhibiting a combination of ancient or derived but parallel morphotypes, and thus, (3) that, one or more of these orders, while showing the general Hamamelid syndrome of anemophily, etc., perhaps may belong in other subclasses (see Table 1). Tiffney (1986) also indicated that there is little or no overall phyletic correlation in fruit dispersal mechanisms in the

TABLE 5. Compound distribution in taxa of the Hamamelidae sampled for phenolics and flavonoids.[a]

Taxon	Phenolics		Flavonols			Flavones				Glycoflavones			Flava-nonols	
	GA	EA	M	Q	K	A	L	T	D	A	L	C	DQ	DK
Trochodendraceae														
Trochodendron araliensis				+	+									
Tetracentraceae														
Tetracentron sinense				+	+								+	
Cercidiphyllaceae														
Cercidiphyllum japonicum	+	+		+	+									
Eupteleaceae														
Euptelea pleiospermum				+	+									
E. polyandra				+	+									
Platanaceae														
Platanus acerifolia				+	+									
P. occidentalis				+	+	+								
Hamamelidaceae														
Corylopsis spicata		+	+	+	+									
C. pauciflora		+	+	+	+									
C. sinensis (2 vars.)	+	+		+	+									
Distylium lepidotum	+	+		+	+								+	+
D. racemosum				+	+									
Fortunearia sinensis				+	+									
Fothergilla major	+	+	+	+	+								+	
F. gardenii	+	+	?	+	+								+	
Hamamelis vernalis	+	+	+	+	+									
H. virginiana	(+)		+	+	+	+				+	+		?	
H. macrophylla	+			?		+				+	+		?	
Liquidambar styraciflua		+	+	+	+								(+)	
L. formosa			+	+	+								(+)	
Loropetalum chinense		+	+	+	+								(+)	
Sycopis sinensis	(+)	+	+	+	+									
Parrotia persica				+	+									
Sinowilsonia henryii	+	+								+	+			
Myrothamnaceae														
Myrothamnus flabellifolium	+	+	+	+	+					?	?			
Daphniphyllaceae														
Daphniphyllum teigmensis				?	?	+	+							
D. glaucescens				?	?	+	+							
D. calycinum				?	?	+	+							
Didymelaceae														
Didymeles spp.	(unknown?)													
Eucommiaceae														
Eucommia ulmoides				+	+									
Barbeyaceae[b]		+		+	+									
Ulmaceae[b]		+	+	+	+	+	+			+	+			
Cannabaceae[c]														
Humulus americana			+	+	+									
H. japonicus				+		+	+			+	+			

TABLE 5. Continued.

Taxon	Phenolics		Flavonols			Flavones				Glycoflavones			Flava-nonols	
	GA	EA	M	Q	K	A	L	T	D	A	L	C	DQ	DK
Moraceae														
Broussonettia papyrifera						+	+			+	+	?		
Cudrania tricuspidata				+	+					+			+	
Dorstenia foetida							+			+	+			
Fatoua specium				+										
Ficus aurea				+	+									
F. benjamina					+									
F. brevifolia				+	+									
F. caprifolia										+				
F. caprica										+				
F. citrifolia				+	+					+				
F. gemina						+	+	+		+	+			
F. laevigata				+	+									
F. llewellynii				+	+									
F. macrophylla				+	+									
F. nitidifolia				+	+									
F. pumila					+									
F. webbiana					+									
Helicostylis elegans				+						+	+			
H. scabra										+	+			
Morus alba				+	+		+							
M. rubra				+	+									+
Cecropiaceae														
Cecropia peltata										+	+			
Pourouma phaeotricha				+	+									
P. palmata										+	+			
Urticaceae														
Boehmeria cylindrica				+	+									
Laportea canadensis			+	+	+	+								
Urtica dioica (2 vars.)				+	+					?				
Leitneriaceae														
Leitneria floridana			+	+	+	+	+			?				
Juglandaceae[d]	+	+	+	+	+					?				+
Rhoipteleaceae														
Rhoiptelea chiliantha		+	+	+	+									
Myricaceae														
Myrica asplenifolia (= *Comptonia perigrina*)		+	+	+	+									
M. cerifera			+	+	+									?
M. gale		+	+	+	+									
M. heterophylla			+	+	+									
M. inodora			+	+	+									+
M. rubra			+	+	+									+
M. serrata		+	+	+	+									+
Balanopaceae														
Balanops	(unknown ?)													

TABLE 5. Continued.

Taxon	Phenolics		Flavonols			Flavones				Glycoflavones			Flava-nonols	
	GA	EA	M	Q	K	A	L	T	D	A	L	C	DQ	DK
Fagaceae														
Quercus[c]		+		+	+	+	+			+			+	
Castanea[c]		+		+									+	
Fagus[f]				+	+									
Betulaceae[g]														
Betula	+		+	+	+	+	+			(+)				
Casuarinaceae[h]														
Casuarina equisetifolia	+		+	+	+									
C. glauca	+		+	+	+								+	
C. cunninghamia	+		+	+	+								+	

[a] Abbreviations: GA = gallic acids, EA = ellagic acids, M = myricetin, Q = quercetin, K = kaempferol, A = apigenin, L = luteolin, T = tricin, D = diosmetin, C = chrysoeniol, DQ = dihydroquercetin, DK = dihydro-kaempferol, + = present, (+) = trace amounts or occasionally present, ? = not completely confirmed.

[b] See Giannasi (1978) for detailed distributions and Table 2. Also see Bate-Smith and Richens (1973).

[c] See also Clark and Bohm (1979).

[d] See Table 3 (Giannasi & Niklas, unpubl. data).

[e] See Niklas and Giannasi (1978).

[f] See Giannasi and Niklas (1981).

[g] See also Wollenweber (1975). Present study also includes some methylated and/or 6-substituted flavones and flavonols as per Wollenweber.

[h] See also Saleh and El-Lakany (1979).

Hamamelidae and similar suggestions may be gleaned from discussion of pollination mechanisms (Whitehead, 1969). Indeed, protein serology (Petersen & Fairbrothers, 1983, 1985) suggests that the affinities of the Leitneriales, for example, lie near or within the Simaroubaceae (Rosidae, sensu Cronquist, 1981). Any one of the alternatives is possible for each of these peripheral orders, especially since most of these orders are monotypic or at least monogeneric. Often there are fewer intermediates that might more clearly suggest more direct interordinal relationships.

In addressing the flavonol bias of some earlier literature, it may be observed from Table 5 that the glycoflavones represent a second major class of flavonoids occurring in the Hamamelidae. As indicated in Tables 4 and 5, these flavonoids, either exclusively or in combination with flavonols and/or flavone O-glycosides, characterize a number of species and genera in various families. This is especially striking in the Daphniphyllaceae in which glycoflavones occur exclusively; a character state considered advanced or derived over the presence of flavonols alone or the intermediate state of flavonols/glycoflavones (e.g., Leitneriaceae). The same trends (i.e., flavonols → glycoflavones) may also be observed at various taxonomic levels within orders (Urticales), families (Moraceae), and genera (*Hamamelis, Ficus*) and thus may represent the major chemical trend of advancement within the subclass. This contrasts with earlier literature, which state that flavonols characterize the Hamamelidae as a whole, implying more of a conservative flavonoid capability than really exists. Exceptions do exist, as in the Betulaceae, for example. In *Alnus, Ostrya,* and especially *Betula,* flavonoids from bud scale excretions contain a large number of variously methylated and 6-substituted derivatives of the flavonols quercetin and kaempferol and to a much lesser degree flavones (apigenin) and flavanones (naringenin). Many of these compounds also occur in the leaves of *Betula* species (Giannasi, unpubl. data) along with the more archaic myricetin glycosides, which apparently do not occur in the bud excretions. Thus, the Betulaceae have retained primitive characters (flavonols) along with specialized characters (6-substitution, 6-methylation, flavones). These highly specialized flavonoids apparently do not commonly occur in the related members of the Fagaceae that have been surveyed (Niklas & Giannasi, 1978; Giannasi & Niklas, 1981; Gian-

TABLE 6. Summary distribution of phenolics and flavonoids in the Hamamelidae (taxonomy follows that of Cronquist, 1981).[a]

Taxon	Phenolic and Flavonoid Distributions[b]																						
	EA	GA	PC	CH	M	Q	K	R	IR	DHF	F6L	GF	A	L	T	AM1	AM2	LM1	LM2	PF	BF	FV	F5M
Trochodendrales																							
Tetracentraceae				+		+	(+)		(+)	(+)													
Trochodendraceae			+			+	+																
Hamamelidales																							
Cercidiphyllaceae	+	+		+		+	+																
Eupteleaceae				+	+	+	+																
Platanaceae			+		+	+	+						+										
Hamamelidaceae	+	+	+		+	+	+			+		+	+										
Myrothamnaceae	+			+		+	+																
Daphniphyllales																							
Daphniphyllaceae						?	?						+	+									
Didymelales																							
Didymelaceae	(unknown ?)																						
Eucommiales																							
Eucommiaceae				+		+	+																
Urticales																							
Barbeyaceae						+	+																
Ulmaceae	+		+		+	+	+			+		+											
Cannabaceae			(+)	+	(+)	+	+			+		+	+							+		+	
Moraceae			+	+	+	+	+		(+)	+		+	+	+	(+)					+		+	
Cercropiaceae			(+)									+											
Urticaceae			+		+	+	+					+		+									
Leitneriales																							
Leitneriaceae					+	+	+						+	+									
Juglandales																							
Juglandaceae	+		+		+	+	+			+		?										+	+
Rhoipteleaceae	+				+	+	+																
Myricales																							
Myricaceae	+		+	+	+	+	(+)																

TABLE 6. Continued.

Taxon	Phenolic and Flavonoid Distributions[b]																								
	EA	GA	PC	CH	M	Q	K	R	IR	DHF	F6L	GF	A	L	T	AM1	AM2	LM1	LM2	PF	BF	FV	F5M
Fagales																									
Balanopaceae	(unknown ?)																								
Fagaceae	+		+	+	+	+	+		+	+	+	+	+	+		+	+	+	+			+	+		
Betulaceae	?		+	+	+	+	+			+	+										+				
Casuarinales																									
Casuarinaceae	+		(+)		+	+	+																		

[a] See text and Table 5 for chemical authorities, especially Bate-Smith (1962), Kubitzki and Reznik (1966), and Gornall et al. (1979).
[b] Compound identification: EA = ellagic acid, GA = gallic acid, PC = proanthocyanidins, M = myricetin, Q = quercetin, K = kaempferol, R = rhamnetin, IR = isorhamnetin, DHF = dihydroflavonols, F6L = flavonol-6 or 8 substituted, GF = glycoflavones, A = apigenin, L = luteolin, T = tricin, AM1 = 7.4′ OMe-apigenin-1, AM2 = 6/8 OMe-apigenin-2, LM1 = 3′4′7 OMe-luteolin-1, LM2 = 6-OH/OMe-luteolin-2, PF = prenylflavonoids, BF = biflavonyls, FV = flavanones, F5M = 5-OMe flavonoids.

nasi, unpubl. data). Therefore, at this time, these compounds in the Betulaceae seem to represent a unique event in the Hamamelidae.

Also notable is the occurrence of a large number of flavones (and a few xanthones) that are substituted at various positions by isoprene (5C) units rather than sugars, methoxy or sulfate units in the root bark of Moraceae (e.g., Nomura et al., 1976, 1977, 1978a, 1978b; Konno et al., 1977; Deshpande et al., 1973). Similarly substituted flavones (or flavanone or flavanonol analogues) also are found in the Rosidae (Fabaceae, Rutaceae) and Asteridae (Asteraceae) and thus are not unique to the Hamamelidae but are unique within a single family of the Hamamelidae. That most of these prenylated flavones in the Hamamelidae have thus far been isolated only from root bark tissue of the Moraceae further emphasizes the possibility of inter-tissue chemical differences, which eventually must be considered in chemical studies (Gornall et al., 1979). Indeed, leaf flavonoids, in this case glycoflavones, seem to be "normally" substituted with C-glycosyl sugars. The occurrence of these prenylated flavones in the Moraceae may represent simply an isolated specialization in the Hamamelidae, as is suggested by the isolated occurrence of biflavonyls in the Casuarinaceae. The latter compounds, too, are unique to the Casuarinaceae in the Hamamelidae but do occur in other subclasses (Rosidae, Dilleniidae). The possibility that the Moraceae do not belong in the Hamamelidae is also possible (see p. 433 for additional discussion). Their scattered occurrence within the angiosperms makes them of questionable taxonomic value at this time.

HAMAMELIDAE—GENERAL CONSIDERATIONS

The Hamamelidae, in terms of their phenolics, seem to represent a primitive group in the general presence of proanthocyanidins, ellagic acid, myricetin compounds, and a general conservatism in other flavonoids. Variation is based on glycosylation patterns of a few simple flavonol and flavone types with a moderate substitution, in some cases, by the evolutionarily intermediate glycoflavones. Proanthocyanidins, ellagic acid, and myricetin flavonoids are considered primitive chemical characters and are often found to be characteristic of woody plants (Bate-Smith, 1962; Harborne, 1977). Thus, the Hamamelidae are distinct from the Magnoliidae and Liliopsida, which generally lack one or more of these compounds. Yet these same Hamamelid characters

are found to some degree among the Rosidae and Dilleniidae, suggesting a more than casual relationship. The predominance of these chemical characters in the Hamamelidae, however, act more as a mark of exclusion of other subclasses because of the preponderance of their occurrence in the Hamamelidae, rather than as any absolute qualitative distinction (or requirement of "primitiveness"). Since non-chemical characters are often used similarly, such correlations among chemical characters are probably just as legitimate. For example, recent ultrastructural studies of phloem sieve-tube plastids show the uniform presence of the S-type in the Hamamelidae (with the exception of *Ulmus* species), but the same type is also found in some Magnoliidae and Rosidae (Behnke, 1973, 1977).

The problem of production of rather rare and unusual compounds in the Hamamelidae (especially the Moraceae), which are of restricted taxonomic use, has already been mentioned. Difficulties arise in the use of chemical data only in their simple distributional form without any consideration of the classes of compounds involved. For example, if the Hamamelidae are characterized by primitive phenolics that are either absent or only moderately represented in the other subclasses, then the Hamamelidae must be a more primitive group (at least with respect to certain secondary compounds) and the others advanced, generally showing a decrease or loss in synthesis of these compounds (cf. Kubitzki & Gottlieb, 1984a, 1984b). Also, the older surveys portray the Magnoliidae and Hamamelidae as being primitive in their flavonoid chemistry due to the overwhelming reporting of flavonols. Yet recent studies on the Winteraceae (Williams & Harvey, 1982), Idiospermaceae (Sterner & Young, 1980), and the Eupomatiaceae (Young, 1983) show not only the presence of flavones in these taxa but also a number of methylated flavones, both advanced characters. If, in fact, flavones and methylated flavones are common in the Magnoliidae, this, along with the absence of the primitive myricetin and ellagic acid (or nearly so), actually suggests a less primitive taxonomic position for the Magnoliidae, and that the more primitive Hamamelidae are not a derivative of the Magnoliidae (sensu Cronquist). Closest chemical similarities of the Hamamelidae lie with some Rosidae, Dilleniidae, and a few Asteridae that have similar compounds, but again, in decreasing amounts (evolution by loss) indicating a more direct relationship with these taxa, or at least parallel biosynthetic capability (Kubitzki & Gottlieb, 1984a, 1984b). To put it simply, one cannot delineate a group (Hamamelidae) as having primitive chemistry and then have it evolve from a group that is possibly more advanced (Magnoliidae) in its chemistry. Alternatively, the possibility still exists that early in their evolution the Hamamelidae and the Magnoliidae may have been more similar in concentrating on synthesis of phenolics. Subsequently, the Magnoliidae and Hamamelidae may have diverged, with the latter retaining emphasis on more primitive phenolics, and the former emphasizing alkaloid synthesis and advanced types of flavonoid substitutions. This, however, is a larger hypothetical "if" (and not provable) than the former alternative, which like all current studies at least deals with factual, contemporary, comparative data. Even in the alternative case, common divergence, rather than derivation, is the logical conclusion to be drawn. Indeed, Kubitzki and Gottlieb (1984a) suggest that the neolignans of the Lauraceae and reduced virolane flavonoid types of the Myristicaceae may represent remnants of an earlier protoangiosperm emphasis on shikimic acid (phenolic) synthesis in these members of the Magnoliidae, where benzylisoquinoline alkaloids are generally absent.

Other compounds (Table 7) such as glucosinolates, sesquiterpene lactones, and polyacetylenes are either limited or erratic in distribution among the angiosperms, providing limited general clarification in angiosperm systematics. However, if we examine biosynthetic and distributional aspects of the nitrogen-containing compounds among the angiosperm subclasses, several interesting comments can be made.

Much has been made of the benzylisoquinoline alkaloids as being characteristic of the Magnoliidae. These compounds (Fig. 6) are derived from aromatic amino acid synthesis. Related isoquinoline and similar types are found in many of the monocots, and apparently in the Caryophyllidae as well. Indeed, if one considers the tyrosine-derived betalains simply as colored alkaloids (Mabry, 1977), then these three taxonomic subclasses are closely related in their biosynthetic origin for these compounds. The Hamamelidae lack these tyrosine-derived alkaloids (at least by present surveys) and thus appear to be less than a direct offshoot of the Magnoliidae. Instead, the Hamamelidae produce mostly nonaromatic amino acid derived alkaloids (Fig. 4) emanating from the citric acid cycle (TCA) or

TABLE 7. Summary of secondary chemistry of angiosperms.

Taxon	Compounds[a]												
	EA	V	FL	FO	OM	GF	BF	G	CGN	AK	I	S	P
Liliidae	–	(+)	Q,K	+	+	+	+	–	O (Ac/k)	O (Ac/k)	–	–	–
Magnoliidae	–	(+)	Q,K (M)	+	+	+	(+)	–	O (Ac/k)	O	–	+	+
Caryophyllidae	–	(+)	Q,K	+	+	+	–	(+)	O	O	–	(+)	–
Hamamelidae	+	+	M,Q,K	(+)	+	+	+	–	Ac/k	Ac/k	+	–	–
Dilleniidae	+	+	M,Q,K	+	+	+	+	+	Ac/k	Ac/k	+	+	–
Rosidae	+	+	M,Q,K	+	+	+	+	+	Ac/k O	Ac/k O	+	+	+
Asteridae	(+)	(+)	Q,K (M)	+	+	+	+	–	Ac/k (O)	Ac/k	+	+	+

[a] Abbreviations: + = present, – = absent or unknown, (+) = isolated occurrence, EA = ellagic acid, V = *vic*-hydroxylation (= trihydroxylated phenolic ring), FL = flavonols, M = myricetin, Q = quercetin, K = kaempferol, FO = flavones, OM = O-methyl flavonoids, GF = glycoflavones, BF = biflavonyls, G = glucosinolates, CGN = cyanogens, AK = alkaloids, O = aromatic-tyrosine or phenylalanine precursor, Ac/k = non-aromatic amino acid precursor from acetate or Krebs (TCA) cycle, I = iridoids, S = sesquiterpene lactones, P = polyacetylenes.

FIGURE 6. Alkaloid types in the Magnoliidae.

carbohydrate precursors. This is much more like the Rosidae, Dilleniidae, and Asteridae, in which tyrosine-derived alkaloids are absent or begin to decrease in representation in favor of TCA-derived alkaloid precursors, or more importantly in some other groups, toward exploitation of the terpene-steroid-derived pseudoalkaloids. Also, of course, not all Magnoliidae produce isoquinoline alkaloids either.

Consideration of cyanogenic glycosides, however, does suggest a relationship between Hamamelidae and Magnoliidae. Those aromatic cyanogens derived from tyrosine (Fig. 7) are found in the Hamamelidae, Magnoliidae, and Liliidae (Liliopsida) as well as in some Rosidae and Asteridae (Saupe, 1981). Oddly enough, those cyanogens derived from phenylalanine occur in ferns and predominate in advanced angiosperm groups, the Rosidae and Asteridae. The gymnosperms produce tyrosine derived cyanogens like the Magnoliidae-Hamamelidae-Liliidae (Liliopsida). Also non-aromatic cyanogens (valine-leucine, isoleucine) begin to predominate in the Rosidae, Dilleniidae, and Asteridae, and thus may represent the more advanced forms restricted to advanced taxonomic groups, a trend not unlike that observed in the evolution of alkaloids from aromatic to non-aromatic precursors. At least in the cyanogens a more direct relationship between Hamamelidae and Magnoliidae is suggested, although it would be interesting to see if the Ham-

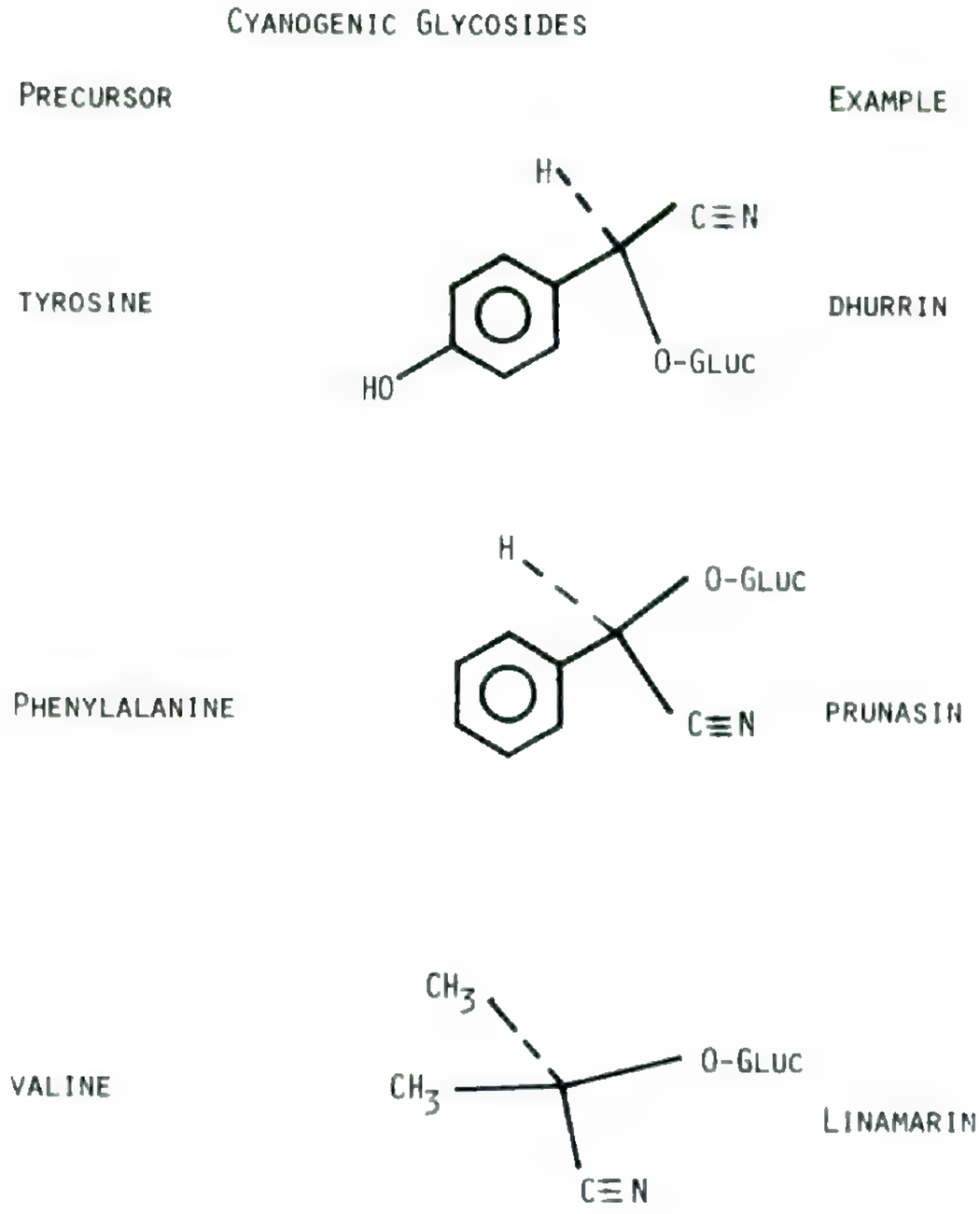


FIGURE 7. Major classes of cyanogenic glycosides in angiosperms and their biogenetic precursors.

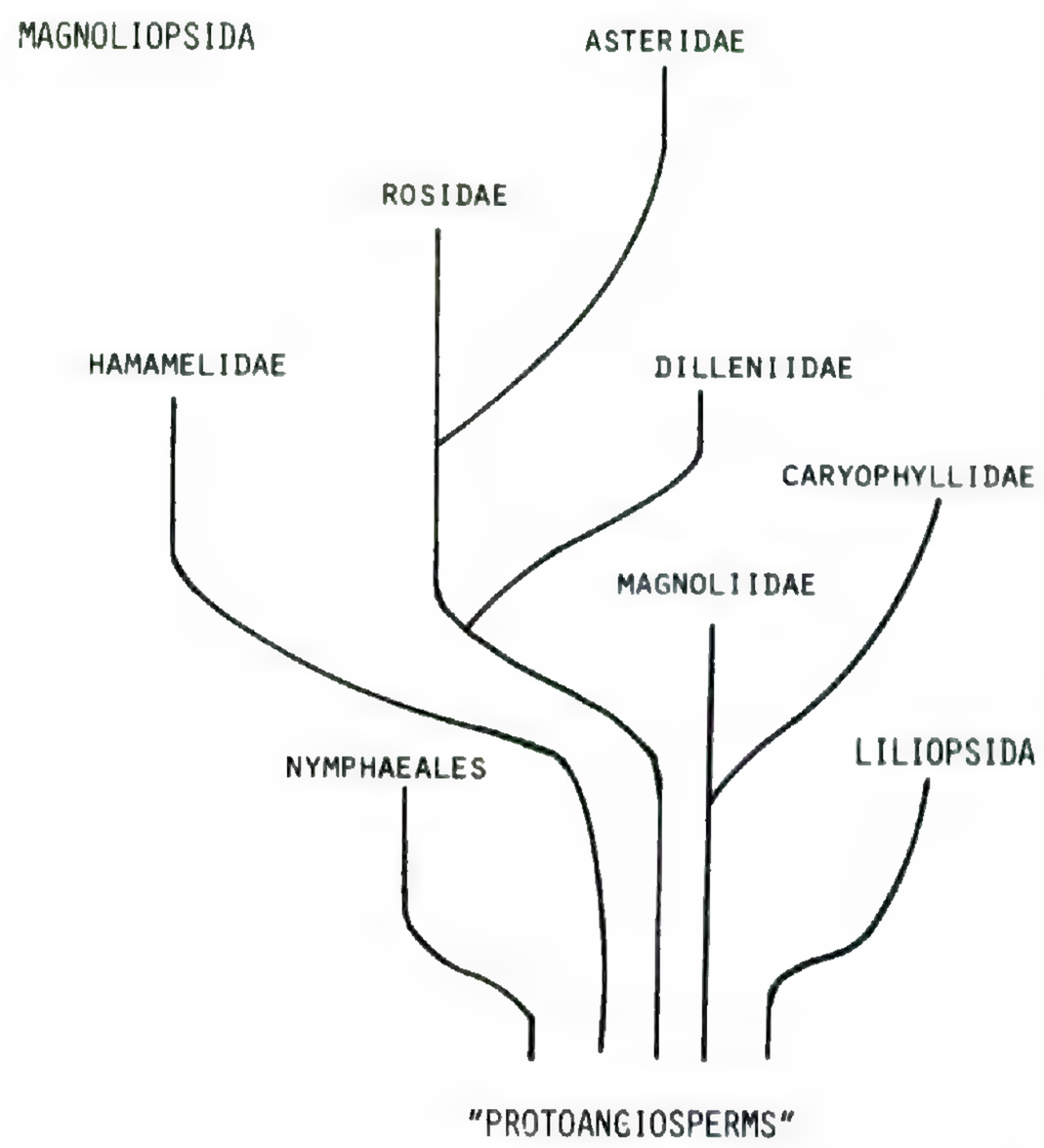


FIGURE 8. Phylogenetic relationship of the Hamamelidae to other subclasses (sensu Cronquist, 1981) based on micromolecular data.

amelidae contain more than one type of aromatic cyanogen and perhaps both aromatic and non-aromatic types. However, among angiosperms there is an overlap in cyanogen types between subclasses (and non-angiosperm seed plants), depending, of course, on the placement of certain taxa within one of the current angiosperm classifications. Thus, some caution should be exercised in emphasizing the systematic significance of these compounds.

Finally, in terms of iridoids, these monoterpene lactone glycosides occur in all of Cronquist's subclasses except Magnoliidae, Caryophyllidae, and Liliidae (Liliopsida). In this case the Hamamelidae are again isolated from the Magnoliidae with suggested similarities closer to the Rosidae.

Looking at Table 7 again, and considering the limitations in conclusions to be drawn from available phytochemical data, I would make the following statements: (1) the Hamamelidae appear to be a primitive subclass of plants at least as old as the Magnoliidae if not older and perhaps not as directly related to the Magnoliidae as suggested, (2) the presence of a number of compounds suggest some similarity (affinity) with the Rosidae/Asteridae, at least at a primal level (this is not new, considering the free movement of taxa by taxonomists between the Hamamelidae/Magnoliidae ↔ Rosidae), (3) the number of unique and highly modified compounds found in some Hamamelidae reinforce the notion of an early divergence of the Hamamelidae from the other subclasses and (4) the current concept of angiosperm monophylesis in the simple sense of a single botanical "Noah's Ark" may require a slightly larger boat or a small but closely integrated fleet, that is, a broader concept of the angiosperm ancestral pool rather than limitation to the Magnoliidae alone (cf. Dilcher, 1979; Retallack & Dilcher, 1981).

The data would suggest an arrangement like that shown in Figure 8, a conclusion similar, at least in part, to the cladistic analysis of non-chemical data for these subclasses by Nixon (unpubl. data), and to conclusions drawn in earlier studies (e.g., Hegnauer, 1977). More recent publications have also come to similar conclusions when attempting to put micromolecular data within biosynthetic and distributional frameworks, recent papers by Kubitzki and Gottlieb (1984a, 1984b), being the most thoughtful and provocative discussions of the problem.

A considerable obstacle to the acceptance of

this argument is the conflict between phytochemistry and palynology. Dilcher (1979) suggests that the reduced, anemophilous, unisexual flower types on catkin-like inflorescences that are found in some possible angiosperm-like Cretaceous fossils represent an alternative ancestral type for modern Hamamelids. However, although the pollen in these fossils may have been wind borne they are monosulcate. Thus they are similar to the earliest presumably angiosperm monosulcate pollen types as found in the Magnoliidae. The presumably more advanced triaperturate pollen of the Hamamelids does not occur as early in the fossil record. Based on pollen distributions then, Hamamelidae still are currently considered to be a derived group (from the Magnoliidae). The problem of opposition in two essentially single morphological character approaches (as well as micromolecules versus pollen) seems insoluble at this point. However, just as phytochemical conclusions may change with each survey, so too each new palynological find may alter current concepts.

The chemotaxonomic debate is by no means finished either, as evidenced by the recent serological review of the angiosperms by Jensen and Greven (1984). These authors indicate that their serological results support a conservative monophylesis of the angiosperms (including the Hamamelidae) from a Magnoliid ancestral group. Interestingly, these serological data also suggest that the Betulaceae are a discordant taxon within the Fagaceae (as do flavonoids), showing a greater similarity to the Magnoliidae. Certainly the rather complex flavonoid chemistry of the Betulaceae (Table 6) does set the family apart within the Fagaceae and the Hamamelidae as well. The same discordance may be cited for the Moraceae (and perhaps the Urticaceae; cf. Table 6), whose flavonoid chemistry is quite unusual within the Urticales and the Hamamelidae generally. Serological work by Petersen and Fairbrothers (1985), in fact, suggests that the Moraceae, Cannabinaceae, and perhaps Urticaceae as well, do not fit in the Hamamelidae, but are better placed near or in the Malviflorae (sensu Dahlgren et al., 1981). Certainly the isoprenyl flavonoids in the Moraceae are found elsewhere only in taxa of the Rosidae/Dilleniidae (sensu Cronquist) lines.

Jensen and Greven (1984) discussed interrelationships among other subclasses as well, and indicated that an expanded survey is desirable (only three taxa tested from the Hamamelidae). Further, they recognized the possibility of changes in their interpretation with the inclusion of more taxa in the test sample. Some considerable variation in precipitation reactions was observed among species from the same genus (*Passiflora*) with the *Magnolia* seed protein employed. Similar exceptional reactions were also observed in some families (Solanaceae). These exceptions and the use of a single seed storage protein still argue for caution in the interpretation of these data.

It is clear from both micro- and macromolecular studies that the Hamamelidae (sensu Cronquist) probably still do not represent a totally natural and homogeneous taxon, and both micromolecular and macromolecular data have much to contribute towards the taxonomic refinement of the concept of the Hamamelidae.

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APPENDIX I

Voucher specimens used in chemical studies.

Trochodendron aralioides Sieb. & Zucc.
UGA Botanical Garden, cultivated
Tetracentron sinense Oliv.
Fang 2725, 6705 (NY)
Cercidiphyllum japonicum Sieb. & Zucc.
Murata et al. 37168, Wood & Boufford 3929 (GA)
Euptelea pleiospermum Hook. f. & Thomas
Brooklyn Botanic Garden, cultivated
E. polyandra Sieb. & Zucc.
Boufford 22245, Murata 44430 (GA)
Platanus acerifolia Willd.
UGA Campus, cultivated, *Shugrue 55* (GA)
P. occidentalis L.
UGA Campus, cultivated
Corylopsis spicata Sieb. & Zucc.
Brooklyn Botanic Garden
C. sinensis Hemsl.
Brooklyn Botanic Garden, cultivated
C. pauciflora Sieb. & Zucc.
Brooklyn Botanic Garden, cultivated
Distylium lepidotum Nakai
Murata et al. 320 (GA)
D. racemosum Sieb. & Zucc.
Brooklyn Botanic Garden, cultivated
Fortunearia sinensis Rehd. & E. H. Wils.
Brooklyn Botanic Garden, cultivated
Fothergilla major Lodd
Radford 34675, Stewart 1554, Wilbur 7012 (GA)
F. gardenii Murr.
Duncan 5115 (GA)
Hamamelis vernalis Sarg.
Chase 9928 (GA)
H. virginiana L.
Faircloth 4235 (GA)
H. macrophylla Pursh.
Ewan 21059 (GA)
Liquidambar styraciflua L.
UGA Botanical Garden
L. formosana Hance
UGA Campus, cultivated
Loropetalum chinense (R. Br.) Oliv.
Meyer 16441, Wigginton s.n. 24-XI-51, Coile 2139 (GA)

APPENDIX I. Continued.

Sycopsis sinensis D. Oliver.
Brooklyn Botanic Garden, cultivated
Parrotia persica C. A. Mey.
Brooklyn Botanic Garden, cultivated
Sinowilsonia henryii Hemsl.
Brooklyn Botanic Garden, cultivated
Myrothamnus flabellifolia Welw.
Brass 16132, Cronquist & de Winter 11608 (NY)
Daphniphyllum teijmanensis
Brooklyn Botanic Garden, cultivated
D. glaucescens Blume
Brooklyn Botanic Garden, *Tanaka & Shimada 17827*
D. calycinum Benth.
Brooklyn Botanic Garden, *Levine 1624*
Eucommia ulmoides Oliv.
Brooklyn Botanic Garden, cultivated; *Gillis 14345* (GA)
Humulus americanus Nutt.
Chase 12151 (GA)
H. japonicus Sieb. & Zucc.
Windler & Stastny 4046 (GA)
Broussonetia papyrifera L'Her
GA, Clarke Co., cultivated
Cudrania tricuspidata (Carr.) Bur. ex Lavallee
GA, *Deason s.n. XI-81,* cultivated
Dorstenia foetida Schweinf. (= *D. obovata* Hochst.)
UGA Greenhouses, cultivated
Fatoua villosa (Thunb.) Nakai
Godfrey 72357, Thieret 10227 (GA)
Ficus aurea Nutt.
Stinson 240 (GA)
F. benjamina L.
Brumbach 9711 (GA)
F. brevifolia Nutt.
Scull s.n. 27-I-40 (GA)
F. caprifolia Del.
Russel 2054 (GA)
F. carica L.
Rainwater E8113 (GA)
F. citrifolia Mill.
Brumbach 9770 (GA)
F. gemina Ruiz ex Miq. in Mart.
Rimachi 2790 (GA)
F. laevigata Vahl.
Smith 966 (GA)
F. llewellynii Standl.
Rimachi 1778 (GA)
F. macrophylla Desp.
Stimson 2050, cultivated (GA)
F. nitidifolia Bur.
Bauman-Bodenheim 15156 (GA)
F. perforata L.
Sauleda 3733 (GA)
F. pumila L.
Crawford et al. 959 (GA)
F. webbiana Miq.
Guillaumin 9178 (GA)

APPENDIX I. Continued.

Helicostylis elegans (Macbr.) C. C. Berg.
Rimachi 4029 (GA)
H. scabra (Macbr.) C. C. Berg.
Rimachi 2898 (GA)
Morus alba L.
Faircloth 5308, Redfearn 3712, Clarke Co., cultivated (GA)
M. rubra L.
Duncan 5131, Clarke Co., cultivated
Cecropia peltata L.
Duke 12500 (GA)
Pourouma palmata P. & E.
Rimachi 2724 (GA)
P. phaeotricha Mildbr.
Rimachi 2725 (GA)
Boehmeria cylindrica (L.) Sw.
Adams & Duncan 19488, Hardin 14286 (GA)
Laportea canadensis (L.) Wedd
Pease s.n. 30-VII-58, Pyron & McVaugh 857 (GA)
Urtica chamaedryoides Pursh
Thieret 32699 (GA)
U. dioica L.
Clokey 8322, Swendsen 487 (GA)
Leitneria floridana Chapm.
Demaree 45267E, McDaniel 903; E. L. Richards 9749 (STAR)
Rhoiptelea chiliantha Diels & Handel-Mazzetti
Ching 5840 (NY)
Myrica asplenifolia L. (= *Comptonia perigrina*)
Ahles 75334, Hardin 364, Hunt MA 180 (GA)
M. cerifera L.
Faircloth 3444, Lane 142 (GA)
M. gale L.
Miller E4315, Ahles 89166 (GA)
M. heterophylla Raf.
Hardin & Duncan 14573, 20724 (GA)
M. inodora Bartr.
Faircloth 732, Godfrey & Harrison s.n. 9-III-57 (GA)
M. rubra
Wigginton s.n. 24-XI-51, s.n. 30-XII-52 (GA)
M. serrata Lam.
Russel 2093 (GA)
Casuarina equisetifolia Forst.
Dugger s.n. 29-IX-40, Ward & Crosby s.n. 9-VIII-65 (GA)
C. glauca Sieb. ex Spreng.
Baum & Wilson 161 (GA)
C. cunninghamiana Miq.
Duncan 30462 (GA)

PHYLOGENY OF THE HAMAMELIDAE: TAXONOMIC INDEX

COMPILED BY DAVID L. DILCHER AND DANIEL MACKLIN[1]

Ailanthus, 400, 423
Alfaroa, 367, 368, 422
Alnus, 277, 278, 279, 362 367, 368, 406, 407, 422, 423, 427
Altingia, 325–328, 333–337, 339–345, 351, 356, 367, 368, 378, 380, 399, 418
Altingiaceae, 325, 326, 345
Altingioideae, 348
Amaryllidaceae, 419
Amentaceae, 229
Amentiferae, 227, 229, 325, 417, 418
Ampelocera, 367, 368, 370, 380, 421
Anacardiaceae, 348, 369, 370, 371, 408, 418, 419, 422, 423
Antiquocarya, 404, 405, 410
Aphananthe, 367, 368, 380, 401, 421
Aquilapollenites, 279
Araliopsis, 228
Artocarpus, 410
Asclepiadaceae, 420
Asteraceae, 429
Asteridae, 419, 421, 423, 429, 430, 431, 432
Atriplex, 406, 407
Austrobaileya, 300

Balanocastanon, 238, 250
Balanopaceae, 260, 276, 348, 357, 368, 370, 396, 398, 405, 408, 413, 418, 426, 429
Balanopales, 408
Balanops, 357, 362, 366, 367, 368, 369, 371, 372, 373, 378, 426
Banksites, 401
Barbeya, 355, 361, 367, 368, 371, 372, 373, 374, 378, 380, 421
Barbeyaceae, 260, 348, 355, 366, 368, 370, 371, 396, 398, 401, 407, 418, 425, 428
Becktonia, 402, 403
Betula, 277, 278, 279, 362, 367, 368, 373, 378, 406, 407, 420, 422, 423, 426, 427
Betulaceae, 228, 238, 249, 251, 252, 261, 276, 277, 279, 348, 362, 366, 368, 369, 370, 371, 373, 396, 398, 406, 408, 411, 412, 417, 418, 419, 422, 423, 426, 427, 429, 433
Betulales, 398, 408
Bicameria, 403, 404
Boehmeria, 403, 404, 421, 426, 437
Broussonettia, 402, 403, 424, 426, 436
Brunelliaceae, 371
Bucklandia, 400
Bucklandioideae, 325
Burseraceae, 419
Buxaceae, 371

Callaeocarpus, 241
Cannabaceae, 348, 355, 368, 369, 370, 396, 398, 402, 404, 407, 412, 418, 424, 425, 428
Cannabidaceae, 260, 261
Cannabinaceae, 433
Cannabis, 355, 362, 367, 368, 374, 378, 402
Caprifoliaceae, 419
Carpinicarpus, 407
Carpinus, 362, 406, 407, 423
Carpinuspollenites, 277
Carpites, 403
Carpolithus, 387
Carya, 278, 357, 367, 368, 369, 404, 405, 419, 422
Caryanthus, 404, 405, 410
Caryophyllidae, 421, 430, 432
Casholdia, 398, 404, 405
Castanea, 229–233, 238–245, 248, 250, 251, 252, 263, 264, 272, 277, 279, 284, 285, 288, 290, 292, 293, 295, 366, 367, 368, 405, 406, 426
Castaneae, 229, 230
Castaneoideae, 230, 231, 234, 239, 240, 241, 245, 250, 251, 252, 262, 263, 268, 272, 279, 359
Castaninae, 230
Castanopsis, 230, 231, 232, 239–246, 248–252, 262, 268, 272, 284, 285, 288, 293, 294, 295, 367, 368, 406
Castanoxylon, 239
Casuarina, 362, 366, 367, 368, 378, 406, 419, 424, 426, 437
Casuarinaceae, 260, 277, 279, 348, 362, 368–372, 396, 398, 406, 407, 411, 418, 424, 426, 429
Casuarinales, 276, 362, 366, 367, 398, 418, 424, 429
Cathayambar, 328, 329, 343
Cecropia, 424, 426, 437
Cecropiaceae, 260, 348, 357, 394, 396, 398, 403, 408, 410–413, 418, 424, 426, 428
Celtidaceae, 421
Celtidoideae, 355, 366, 369, 370, 371, 401, 402, 409
Celtis, 362, 367, 368, 373, 380, 401, 402, 421
Cercidiphyllaceae, 260, 279, 319, 348, 349, 367, 370, 373, 382, 393, 396, 398, 399, 407, 418, 425, 428
Cercidiphyllales, 349, 382
Cercidiphyllites, 277
Cercidiphyllum, 297–300, 303–309, 312, 313, 315–321, 349, 351, 367, 368, 378, 380, 382, 383, 385–393, 399, 425, 436
Cerris, 232, 247, 261, 262
Chaetachme, 367, 368, 380, 421
Chaetacme, 401
Chaetoptela, 401, 421
Chaetoptelea, 367, 368, 370
Chloranthaceae, 225, 236
Chlorophora, 402, 403
Chrysolepsis, 230, 231, 232, 240, 241, 242, 246, 250, 251, 252, 261, 264, 268, 272, 367, 368
Chunia, 342, 353
Chunioideae, 325
Clusiaceae, 419
Complexiopollis, 375
Comptonia, 404, 407
Corylaceae, 423
Corylocarpinus, 407
Corylopsis, 278, 305, 353, 356, 367, 368, 378, 380, 400, 425, 436
Corylus, 278, 362, 367, 368, 406, 407, 408, 423

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Coussapoa, 410
Cryptocarya, 420
Cudrania, 402, 410, 424, 426, 436
Cupuliferae, 229, 230
Cupuliferites, 239
Cyclobalanopsideae, 230
Cyclobalanopsis, 230, 232, 243, 246, 247, 250, 262
Cyclobalanus, 230
Cyclocarya, 398, 404, 405, 410

Daphniphyllaceae, 260, 348, 353, 368, 370, 371, 396, 398, 400, 408, 411, 413, 418, 420, 425, 427, 428
Daphniphyllales, 227, 353, 366, 367, 398, 418, 424, 428
Daphniphyllum, 358, 359, 367, 368, 378, 380, 420, 425, 436
Debeya, 228, 278
Debeya-Dewalquea, 248, 252
Degeneria, 366
Dewalquea, 228
Didymelaceae, 260, 277, 279, 348, 353, 372, 373, 396, 398, 408, 413, 418, 420, 425, 428
Didymelales, 276, 353, 398, 400, 418, 428
Didymeles, 420, 421, 425
Dilleniidae, 369, 408, 419, 421, 429, 430, 431
Diospyros, 233
Disanthoideae, 325, 342, 344, 345, 353
Disanthus, 326, 342, 353, 356, 367, 368, 378, 380, 382, 400, 418
Distinctae, 248
Distylium, 353, 400, 425, 436
Dorstenia, 357, 362, 367, 368, 369, 378, 402, 411, 424, 426, 436
Dryophyllum, 233, 239, 242, 245, 252, 278, 279

Embothrites, 401
Engelhardtia, 357, 367, 368, 404, 405, 410, 422
Engelhardtieae, 369
Erythrobalanus, 230, 232, 247, 261, 262, 264
Eucastanon, 238, 250
Eucommia, 353, 360, 366, 367, 368, 372, 378, 380, 398, 400, 401, 420, 425, 436
Eucommiaceae, 260, 279, 348, 353, 367, 368, 370, 372, 373, 396, 398, 400, 407, 418, 420, 425, 428
Eucommiales, 353, 398, 418, 424, 428
Euliquidambar, 328
Euphorbiaceae, 408, 418, 419
Euphorbiales, 408, 418
Eupomatiaceae, 430
Euptelea, 297–300, 303–309, 312, 313, 315, 316, 318, 319, 320, 321, 349, 351, 367, 368, 378, 380, 425, 436
Eupteleaceae, 348, 349, 370, 373, 396, 398, 399, 418, 425, 428
Eupteleales, 349
Eupteliaceae, 260, 319
Euquercus, 246, 247
Exbucklandia, 342, 343, 344, 351, 353, 356, 367, 368, 378, 380, 399
Exbucklandioideae, 325, 342, 344, 345, 351

Fabaceae, 429
Fagaceae, 228–232, 234–241, 245, 246, 248–253, 261, 262, 263, 276–280, 284, 285, 295, 296, 348, 359, 366, 368–373, 394, 396, 398, 405, 406, 408–413, 418, 420, 423, 426, 429, 433
Fagales, 276, 357, 366, 367, 408, 417, 418, 423, 424, 429
Fageae, 230
Fagineae, 230
Fagoideae, 229, 230, 233, 250, 251, 262, 263, 268, 362
Fagophyllum, 278, 279
Fagopsis, 229, 236, 251, 252, 278, 280, 398, 405, 406, 408, 409, 410
Fagoxylon, 278
Fagus, 229–234, 237, 238, 239, 245, 250, 251, 252, 261, 263, 277, 278, 280, 284, 362, 366, 367, 368, 374, 405, 406, 417, 426
Fatoua, 426, 436
Ficus, 402, 403, 420, 421, 424, 426, 427, 436
Fortunearia, 400, 425, 436
Fothergilla, 353, 356, 367, 368, 378, 380, 400, 425, 436
Fraxinifolae, 248
Fraxinus, 400

Galumpita, 421
Ginko, 388
Girardinia, 403
Gironniera, 367, 368, 380, 401, 402, 421
Guttiferae, 419
Gymnostoma, 362, 366, 367, 368, 378

Haloragacidites, 277
Hamamelidaceae, 260, 277, 279, 297, 303, 305, 306, 308, 315, 318, 319, 325, 326, 344, 345, 348, 351, 356, 367, 368, 369, 370, 373, 393, 395, 396, 398, 399, 400, 407, 411, 412, 418, 420, 423, 424, 425, 428
Hamamelidae, 225, 226, 227, 276, 277, 297, 303, 309, 315, 321, 322, 348, 366, 369–373, 375, 382, 383, 394, 395, 396, 398, 399, 408, 411, 412, 413, 417–421, 423, 424, 425, 427–433
Hamamelidales, 276, 297, 303, 318, 321, 322, 349, 366, 367, 371, 382, 398, 417, 418, 423, 424, 428
Hamamelidiae, 278
Hamamelididae, 225
Hamamelidiflorae, 370
Hamamelidoid, 278
Hamamelidoideae, 326, 342, 344, 353, 399
Hamamelidopsidae, 237
Hamamelis, 303, 353, 356, 367, 368, 378, 380, 399, 400, 424, 425, 427, 436
Helicostylis, 424, 426, 436
Helicostylus, 424
Hemiptelea, 367, 368, 421
Hemistylus, 411
Hicoreae, 369
Holoptelea, 367, 368, 421
Hooleya, 405
Hortonia, 300
Humularia, 402
Humulus, 402, 424, 425, 436
Hypocastanon, 238

Idiospermaceae, 430
Illicium, 313

Jenkinsella, 319
Joffrea, 319, 382, 383, 385, 387, 389, 391, 392, 393, 399
Juglandaceae, 260, 279, 348, 357, 368–371, 373, 394,

395, 396, 398, 404, 408–411, 413, 417–420, 422, 423, 426, 428
Juglandales, 227, 357, 366, 367, 398, 408, 418, 423, 424, 428
Juglandicarya, 405
Juglandineae, 422
Juglans, 367, 368, 369, 374, 398, 404, 405, 410, 422
Julianaceae, 418, 422

Klikovispermum, 400

Laportea, 403, 404, 426, 437
Lauraceae, 420, 430
Laurales, 306, 419
Leitneria, 227, 353, 360, 367, 368, 371, 372, 374, 378, 404, 424, 426, 437
Leitneriaceae, 261, 348, 353, 368, 370, 371, 373, 396, 398, 404, 407, 418, 424, 426, 427, 428
Leitneriales, 227, 353, 366, 367, 398, 418, 423, 424, 427, 428
Lepidobalanus, 232, 247, 261, 262
Liliaceae, 419
Liliopsida, 419, 421, 429, 431, 432
Lilliidae, 421, 431, 432
Limaipollenites, 375
Limlia, 244, 251
Liquidambar, 277, 325–329, 331, 333–337, 339–345, 367, 368, 378, 380, 399, 400, 418, 420, 425, 436
Liquidambaroideae, 325, 327, 328, 341, 342, 344, 345, 348, 351, 366, 367, 368, 373
Lithocarpeae, 230
Lithocarpus, 230, 231, 232, 239, 240, 242–246, 248–252, 261–264, 268, 272, 284–289, 291–295, 367, 368, 405, 406, 410
Loropetalum, 353, 356, 367, 368, 378, 380, 425, 436
Lozanella, 367, 368, 380, 421

Macrobalanus, 230, 232, 247, 262
Magnolia, 433
Magnoliaceae, 297, 299
Magnoliales, 306, 318, 321, 322, 382, 418
Magnolidae, 321
Magnoliid, 433
Magnoliidae, 227, 297, 303, 309, 315, 321, 322, 394, 418, 419, 420, 421, 422, 429–433
Magnolioid, 278
Magnolipsida, 432
Malvales, 408, 418
Malviflorae, 433
Manningia, 404, 405, 410
Matudaea, 353, 356, 367, 368, 378, 380
Mesobalanus, 232, 247, 261
Metatrophis, 411
Microcarpolithes, 403, 404
Mirandaceltis, 367, 368, 380, 421
Momipites, 277
Moraceae, 260, 261, 348, 357, 366, 369, 373, 394, 396, 398, 402, 403, 404, 408, 410, 411, 412, 413, 417, 418, 419, 420, 424, 426, 427, 428, 429, 430, 433
Moroidea, 402, 403
Morus, 402, 403, 419, 426, 437
Myrica, 277, 279, 357, 362, 367, 368, 369, 379, 404, 419, 420, 424, 426, 437
Myricaceae, 261, 276, 279, 348, 357, 368, 370, 371, 373, 396, 398, 404, 407, 411, 412, 418, 420, 423, 426, 428
Myricales, 276, 357, 366, 367, 398, 418, 423, 424, 428
Myristicaceae, 430
Myrothamnaceae, 260, 318, 348, 349, 366, 367, 368, 370, 372, 396, 398, 400, 407, 418, 425, 428
Myrothamnus, 351, 354, 366, 367, 368, 371, 379, 380, 425, 436
Mytilaria, 342, 344, 351, 353
Mytilarioideae, 325, 342

Nandinaceae, 419
Nordenskioldia, 399
Nothofagaceae, 228, 231, 250, 251, 252, 279
Nothofagidites, 235
Nothofagoxylon, 237, 278
Nothofagus, 228–238, 249–252, 261, 263, 264, 268, 272, 276–281, 348, 362, 366–371, 405, 406
Nymphaeales, 419, 432
Nyssidium, 382, 383, 385, 387, 389, 391, 392, 393, 399

Ochnaceae, 419
Oreomunnea, 367, 368, 422
Ostrya, 362, 406, 407, 422, 423, 427
Ostryopsis, 362, 406
Ovicarpum, 402, 403

Paleocarpinus, 406, 407
Paleooreomunnea, 405
Paraengelhardtia, 405
Parasponia, 367, 368, 369, 380, 421
Parrotia, 305, 353, 400, 425, 436
Pasania, 230, 244
Pasanieae, 230
Pasaniopsis, 244
Passiflora, 433
Phyllites, 237, 245
Phyllostylon, 367, 368, 421
Picrasma, 423
Pilea, 403, 404, 411
Piperales, 419
Pistacia, 362, 367–371, 379
Plagioceltis, 421
Planera, 355, 367, 368, 401, 421
Platanaceae, 260, 278, 279, 318, 345, 348, 349, 367, 368, 370, 373, 396, 398, 399, 407, 413, 418, 425, 428
Platanus, 227, 345, 349, 351, 352, 367, 368, 379, 380, 399, 425, 436
Platycarya, 357, 367, 368, 369, 404, 405, 422
Platycaryeae, 369
Plicapollis, 371
Poaceae, 371
Polyptera, 398, 404, 405
Populus, 362, 367, 368, 369, 370, 379
Pourouma, 424, 426, 437
Pranus, 388
Prisca, 319
Procris, 411
Protobalanus, 232, 247, 248, 262
Prunus, 400
Pseudofagineae, 229, 231, 251
Pseudofagus, 229, 231, 251, 406
Pterocarya, 357, 367, 368, 369, 374, 404, 405, 409, 410, 422
Pteroceltis, 367, 368, 380, 401, 402, 421

Querceae, 230
Quercineae, 229, 230
Quercoideae, 229, 230, 231, 234, 245, 250, 251, 252, 262, 263, 268, 272, 362
Quercophyllum, 248
Quercus, 229–232, 239, 240, 242–252, 261–264, 268, 272, 279, 280, 284, 285, 288, 290, 291, 293, 295, 367, 368, 374, 398, 405, 406, 426

Ranunculaceae, 309
Ranunculidae, 419
Rhamnaceae, 419
Rhodoleia, 326, 342, 343, 344, 351, 356, 367, 368, 374, 379, 380, 399, 400
Rhodoleiaceae, 326
Rhodoleideae, 351
Rhodoleioideae, 325, 342, 344, 345
Rhoiptelea, 357, 367, 368, 369, 374, 426, 437
Rhoipteleaceae, 348, 357, 366, 368–371, 396, 398, 404, 407, 418, 422, 426, 428
Rhoipteliaceae, 260
Rosidae, 419, 421, 423, 427, 429–432
Rosidae-Hamamelidae, 297, 321
Rosideae, 369, 371, 408
Rosiflorae, 422
Rousselia, 410
Rutaceae, 429
Rutales, 418
Rutiflorae, 371, 422
Rutinae, 422

Salicaceae, 227, 348, 369, 370
Salix, 367, 368, 369, 370
Sapindales, 227, 408, 418
Schisandraceae, 309, 418
Schizocolpus, 277
Semiliquidambar, 326, 327, 336, 337, 341–345
Simaroubaceae, 433
Sinowilsonia, 278, 393, 424, 425, 436
Sloetia, 402, 410
Solanaceae, 433
Soleirolia, 410
Steinhauera, 399, 400
Streblus, 410, 411
Suspectae, 248
Sycopsis, 305, 353, 425, 436
Symingtonia, 343
Symingtonioideae, 325

Tetracentraceae, 260, 349, 370, 396, 398, 399, 418, 425, 428
Tetracentron, 278, 297–301, 303–309, 312–315, 318–321, 348, 349, 367, 368, 370, 372, 380, 389, 399, 425, 436
Thymeleceae, 418, 419
Trema, 367, 368, 369, 380, 401, 421
Tricolporopollenites, 277
Trigonobalanoideae, 229, 231, 251
Trigonobalanus, 229–232, 239, 242, 244, 245, 246, 250, 251, 252, 262, 268, 272, 284, 285, 367, 368, 398, 405, 406, 418
Trimeniaceae, 300
Trochodendraceae, 260, 297, 299, 319, 348, 349, 367, 370, 396, 398, 399, 407, 418, 425, 428
Trochodendrales, 297–300, 303, 305, 306, 318–322, 349, 366, 367, 370, 372, 373, 382, 398, 399, 418, 424, 428
Trochodendreae, 297, 319
Trochodendrocarpus, 382, 383, 387, 388, 389, 391, 392, 393
Trochodendron, 297–310, 313–316, 318–321, 349, 368, 399, 425, 436
Tubela, 407
Tylophora, 420

Ulmaceae, 260, 261, 276, 279, 348, 355, 366, 368, 369, 371, 373, 394, 396, 398, 400, 401, 407, 408, 409, 411, 413, 417, 418, 419, 421, 425, 428
Ulmoideae, 355, 369, 370, 401, 402, 409
Ulmus, 277, 278, 362, 367, 368, 401, 421, 430
Urtica, 403, 421, 424, 426, 437
Urticaceae, 260, 261, 348, 357, 366, 373, 394, 396, 398, 403, 404, 407, 408, 410–413, 417, 418, 424, 426, 428, 433
Urticales, 227, 355, 366, 367, 370, 371, 398, 408, 418, 424, 427, 428, 433
Urticicarpum, 403
Urticoidea, 403, 404

Virentes, 263

Winteraceae, 297, 309

Zelkova, 367, 368, 401, 421

PHYLOGENETIC STUDIES USING PROTEIN SEQUENCES WITHIN THE ORDER MYRTALES[1]

P. G. MARTIN[2] AND J. M. DOWD[2]

ABSTRACT

N-terminal sequences (40 amino acids) of ribulose bisphosphate carboxylase small subunit are presented for representatives of Myrtaceae (2 spp.), Melastomataceae (2 spp.), Combretaceae (2 spp.), Lythraceae (2 spp.), Thymelaeaceae (2 spp.), Onagraceae (11 spp.), Buxaceae sensu lato (2 spp.), Euphorbiaceae (2 spp.), and Tiliaceae (2 spp.). In minimal phylogenetic trees the two members of most families pair well, while, in Onagraceae, the phylogenetic tree gives a reasonable approximation to the expectations from taxonomy. The first four families group together as expected for families of Myrtales, but Onagraceae are slightly separate. Thymelaeaceae grouped with the Myrtales families. In order to test the hypothesis that Thymelaeaceae are related to Euphorbiales and both to Malvales, phylogenetic trees embracing all groups were derived. Thymelaeaceae failed to group with Malvales but both showed relationships to Myrtales. Within Euphorbiales and Malvales, grouping of species conformed well with expectations.

A symposium on "The Order Myrtales" was held at the XIII International Botanical Congress in 1981 and, when introducing the published proceedings, Raven (1984) summed up the consensus opinion that this order is a clearly defined group. This suggests that the families that comprise the Myrtales may be favorable subjects for a study in which a comparison is to be made between phylogenies derived from morphological, anatomical, and micromolecular characteristics and from an independent approach such as the computerized analyses of macromolecular sequence data.

The most comprehensive attempt to build an angiosperm phylogeny from sequence data is that of Martin et al. (1985), which combined into a single analysis sequences of four proteins and one RNA for up to 11 families. Phylogenetic trees derived from a single macromolecule did not agree with each other and consistency was maintained only when a fourth macromolecule was added to the combined sequences of three proteins. The explanation advanced for this result was that, for four of the macromolecules (the exception was the small subunit of ribulose bisphosphate carboxylase, henceforth RBC-SSU), a family was often (17 out of 33 cases) represented by only a single sequence. Martin et al. (1985) suggested that errors were less likely if a family node was derived from more than one member of a family. The present investigation was carried out to test this idea that replication is effective, a measure of the correctness of a phylogeny being available in Myrtalean taxonomy. However, in our laboratory it is practicable to sequence only RBC-SSU and there are no sequences of other macromolecules available for the Myrtales. Therefore the test is limited to what is achievable with only one sequence. It can be claimed that, with more sorts of sequence data, greater precision would follow.

MATERIALS AND METHODS

The 27 species that have been investigated are listed by family in Table 1. Methods are set out in detail in Martin and Jennings (1983) and the following is only a very brief account. One hundred grams of fresh leaves were treated using the "pungent-leaf method." After maceration, species of Onagraceae were usually very mucilaginous so that more than the usual amount of extracting buffer was necessary to prevent solidification before gel-chromatography. After purification of the "fraction 1" protein, S-carboxymethylation, and separation of the subunits, five milligrams of small subunit were sequenced on the Beckman Automatic Sequencer 890C. No attempt was made to progress beyond the first 40 amino acids. Amino acids were identified us-

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TABLE 1. Species studied. ABG and MBG indicate that the leaves were collected from plants growing in the botanical gardens at Adelaide (ABG) and St. Louis, Missouri (MBG), respectively. AD indicates that leaves were collected elsewhere and a voucher specimen has been lodged in herbarium AD. For two species collected in the field there were only enough leaves for processing, not for voucher specimens.

Myrtaceae	
Eucalyptus microcarpa (Maiden) Maiden	AD
Acmena smithii Poit.	ABG
Melastomataceae	
Melastoma affine D. Don.	
Tibouchina semidecandra Cogn.	ABG
Combretaceae	
Quisqualis indica L.	MBG
Combretum decandrum Roxb.	ABG
Lythraceae	
Lythrum salicaria L.	ABG
Woodfordia fruticosa (L.) Kurz	ABG
Thymelaeaceae	
Daphne odora Thunb.	ABG
Pimelea physodes Hook.	
Onagraceae	
Ludwigia peploides (Kunth) Raven	AD
Lopezia semeiandra (Plitmann) Raven & Breedlove	MBG
Circaea cordata Royle	MBG
Fuchsia hybrida Voss	AD
Epilobium ciliatum Raf.	AD
Epilobium canum (Greene) Raven	ABG
Hauya elegans DC.	MBG
Clarkia unguiculata Lindl.	AD
Clarkia rubicunda (Lindl.) Lewis & Lewis	AD
Gaura lindheimeri Engelm. & Gray	ABG
Oenothera stricta Ledeb.	AD
Buxaceae sensu lato	
Simmondsia chinensis (Link) Schneid.	ABG
Buxus sempervirens L.	ABG
Euphorbiaceae	
Acalypha wilkesiana Muell. Arg.	ABG
Ricinus communis L.	ABG
Tiliaceae	
Grewia occidentalis L.	ABG
Sparmannia africana L.f.	ABG

ing high pressure liquid chromatography and thin-layer chromatography. Sequence data were analyzed by computer methods that have been described by Martin et al. (1985). Briefly the amino acid sequences were converted to inferred nucleotide sequences from which differences between species were derived. The program estimates the lengths of all possible Steiner trees and the minimal phylogenetic tree is deemed the most probable. Consensus trees are derived from the shortest trees and this procedure is especially important when more than one tree of minimal length occurs. Thus the method is essentially one of maximum parsimony. It should be noted that the number of possible trees increases exponentially with the number of taxa and, with most computers, usually only 11 taxa can be analyzed simultaneously. For taxa that group together constantly no matter what others are present, sequences of their common node can be derived and used in other analyses, so making the tree-building process more practical.

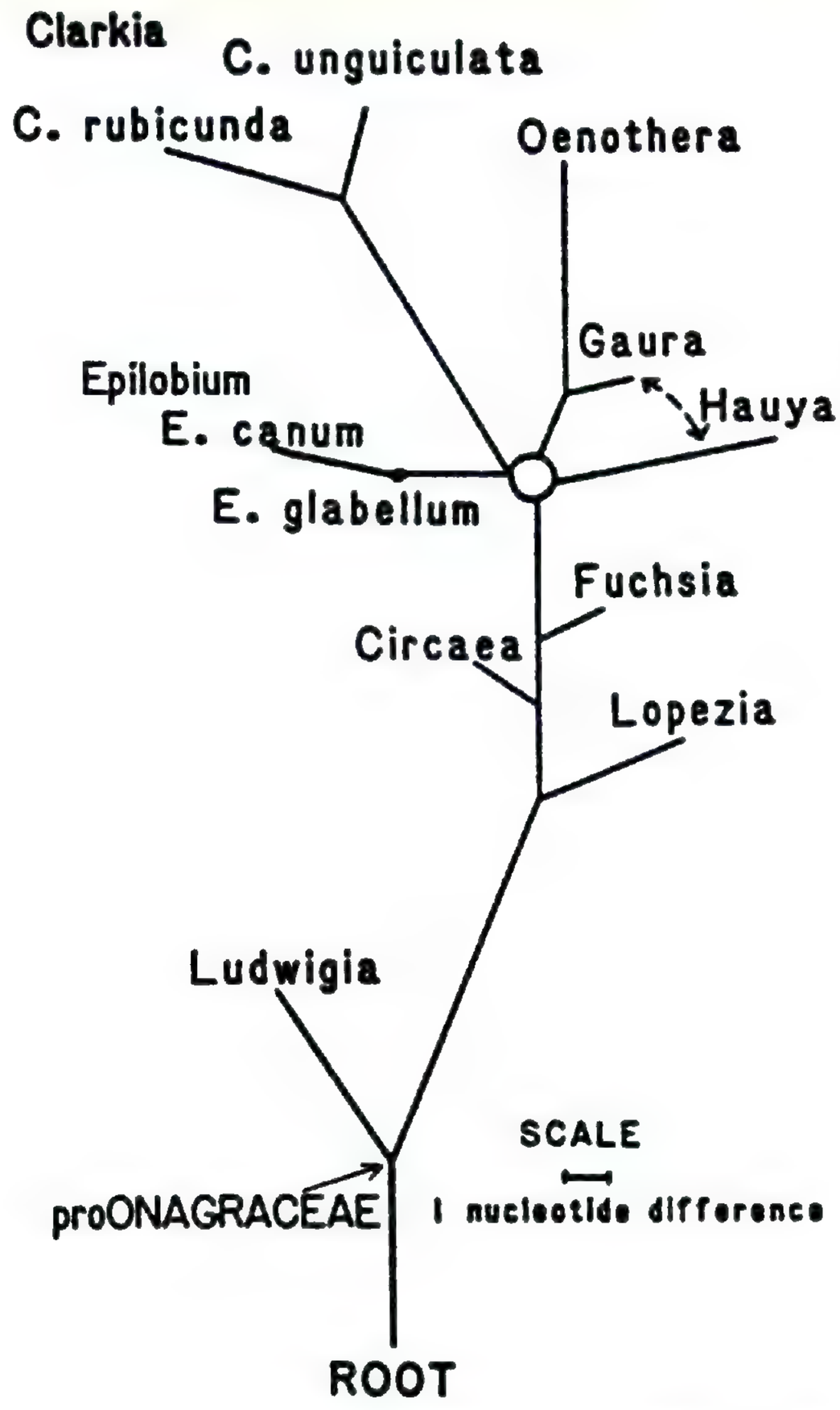

FIGURE 1. Phylogenetic tree for 11 species of Onagraceae. For specific names see Table 1. The two equally probable consensus trees differed in that the branches carrying *Gaura* and *Hauya* were interchanged. Note that in these trees angles are meaningless.

RESULTS

General. N-terminal sequences (40 amino acids) are listed in Table 2. More than 100 other

TABLE 2. N-terminal sequences of RBC-SSU. For other specific names and also names of families see Table 1. A, alanine; D, aspartic acid; E, glutamic acid; F, phenylalanine; G, glycine; I, isoleucine; K, lysine; L, leucine; M, methionine; N, asparagine; P, proline; Q, glutamine; R, arginine; S, serine; T, threonine; V, valine; W, tryptophan; Y, tyrosine.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Eucalyptus	M	Q	V	W	P	P	I	G	K	K	K	F	E	T	L	S	Y	L
Acmena	M	Q	V	W	P	P	T	G	K	K	K	F	E	T	L	S	Y	L
Melastoma	M	Q	V	W	P	P	E	N	K	K	K	F	E	T	L	S	Y	L
Tibouchina	M	Q	V	W	P	P	E	N	K	K	K	F	E	T	L	S	Y	L
Quisqualis	M	K	V	W	P	P	L	G	K	K	K	F	E	T	L	S	Y	L
Combretum	M	K	V	W	P	P	L	G	K	K	K	F	E	T	L	S	Y	L
Lythrum	M	Q	V	W	P	P	E	G	L	K	K	F	E	T	L	S	Y	L
Woodfordia	M	Q	V	W	P	P	L	G	K	K	K	F	E	T	L	S	Y	L
Daphne	M	Q	V	W	P	P	V	G	L	K	K	F	E	T	L	S	Y	L
Pimelea	M	Q	V	W	P	P	T	N	N	K	K	F	E	T	L	S	Y	L
Ludwigia	M	K	V	W	P	P	E	G	K	K	K	F	E	T	L	S	Y	L
Lopezia	F	N	V	W	P	P	E	G	L	L	K	F	E	T	L	S	Y	L
Circaea	F	N	V	W	P	P	E	G	L	K	K	F	E	T	L	S	Y	L
Fuchsia	F	N	V	W	P	P	E	G	L	K	K	F	E	T	L	S	Y	L
Epilobium ciliatum	F	N	V	W	P	P	E	G	L	K	K	F	E	T	L	S	Y	L
Epilobium canum	F	N	V	W	P	P	E	G	L	K	K	F	E	T	L	S	Y	L
Hauya	F	N	V	W	P	P	E	G	K	K	K	F	E	T	L	S	Y	L
Clarkia unguiculata	F	N	V	W	P	P	E	G	L	K	K	F	E	T	L	S	Y	L
Clarkia rubicunda	F	N	V	W	P	P	L	G	L	K	K	F	E	T	L	S	Y	L
Gaura	F	N	V	W	P	P	E	G	L	K	K	F	E	T	L	S	Y	L
Oenothera	F	N	V	W	P	P	E	G	L	K	K	F	E	T	L	S	Y	L
Simmondsia	M	Q	V	W	P	P	L	G	S	K	K	F	E	T	L	S	Y	L
Buxus	M	Q	V	W	P	P	V	G	S	K	Y	F	E	T	L	S	Y	L
Acalypha	M	Q	V	W	P	P	V	G	S	K	Y	F	E	T	L	S	Y	L
Ricinus	M	Q	V	W	P	P	V/L	G	S	K	K	F	E	T	L	S	Y	L
Grewia	M	K	V	W	P	P	I	N	K	K	I	F	E	T	L	S	Y	L
Sparmannia	M	K	V	W	P	T	E	G	L	K	K	F	E	T	L	S	Y	L

species of angiosperms have now been analyzed, from a wide range of families, and so it is possible to say that the range of variation exhibited in Table 2 is quite normal in all respects except one. The occurrence of phenylalanine and asparagine at positions one and two in most species of Onagraceae is unknown elsewhere.

Onagraceae. In Raven's (1979) classification of Onagraceae, *Zauschneria* is combined with *Epilobium* and *Godetia* is combined with *Clarkia*. The results support this taxonomy; preliminary analyses on these sequences showed that *Epilobium canum* (formerly *Zauschneria californica*) grouped closely and consistently with *Epilobium ciliatum*. Similarly *Clarkia rubicunda* (formerly *Godetia amoena*) grouped consistently with *Clarkia unguiculata*. Considering these results, and the taxonomic position, we derived the sequences at generic nodes for *Epilobium* and *Clarkia* and used these in subsequent analyses. This reduced the number of taxa from 11 to nine and for these there were 57 trees of minimal length. This situation arose because there were two adjacent internodes of very short and equal length so that many different combinations were possible without change of overall tree length. For similar reasons there were two consensus trees. We have rationalized the situation and in Figure 1 have presented a single tree with a circle of uncertainty at the relevant node and showing the difference between the two consensus trees. According to Raven (1979) there are seven tribes; Onagreae (represented here by *Clarkia, Oenothera,* and *Gaura*), Epilobieae, and Hauyeae arise from this circle of uncertainty. The remaining four taxa in our analysis represent four monogeneric tribes and the analysis shows them as separate. The point at which other families join into this tree (see below) is taken to be the root of the Onagracean tree and this makes the first divergence between *Ludwigia* and the rest. This is in part because *Ludwigia* is the only species

TABLE 2. Continued.

19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
P	T	L	S	S	E	Q	L	A	K	E	V	D	Y	L	I	K	K	G	W	V	P
P	T	L	S	P	E	Q	L	A	K	E	V	D	Y	L	I	L	S	G	W	V	P
P	P	L	S	S	D	Q	L	L	K	Q	I	A	Y	L	I	N	K	G	W	I	P
P	D	L	S	S	E	Q	L	I	K	Q	I	A	Y	L	I	R	S	G	W	I	P
S	P	L	S	S	Q	Q	L	L	K	E	V	D	Y	L	L	S	N	G	W	V	P
S	P	L	S	Y	E	Q	L	L	K	E	V	D	Y	L	L	A	N	K	W	V	P
P	P	L	T	S	E	E	L	L	K	E	V	E	Y	L	L	L	K	G	W	V	P
P	P	L	T	T	T	Q	L	A	K	E	V	D	Y	L	L	L	K	G	W	V	P
P	P	L	T	S	E	Q	L	A	K	E	I	D	Y	L	I	R	N	K	W	I	P
P	P	L	S	T	V	Q	L	A	K	E	I	E	Y	L	I	R	N	K	W	I	P
P	P	L	T	D	E	Q	L	G	K	E	V	D	Y	L	L	S	K	G	W	V	P
P	P	L	T	Q	E	Q	L	L	K	E	V	D	Y	L	L	S/R	K	N	W	V	P
P	T	L	T	Q	D	Q	L	I	K	E	V	E	Y	L	L	R	K	G	W	V	P
P	P	L	T	Q	E	Q	L	I	K	E	V	E	Y	L	L	S	N	G	W	V	P
P	P	L	T	R	E	Q	L	I	K	E	V	E	Y	L	L	R	N	G	W	V	P
P	P	L	T	R	D	Q	L	G	K	E	V	E	Y	L	L	R	N	G	W	V	P
P	P	L	S	T	E	Q	L	L	K	E	V	E	Y	L	L	R	N	G	W	V	P
P	P	L	T	A	D	Q	L	I	K	E	V	D	Y	L	L	K	K	G	W	V	P
P	P	L	T	T	D	Q	L	I	K	E	V	D	Y	L	L	K	N	N	W	V	P
P	P	L	T	T/D	E	Q	L	I	K	E	V	E	Y	L	I	S	N	G	W	V	P
P	P	L	S	R	E	Q	L	I	K	E	V	E	Y	L	I	R	N	T	W	V	P
P	P	L	S	P	E	S	L	A	K	E	V	E	Y	L	L	L	N	G	W	I	P
P	P	L	T	T	E	Q	L	L	A	E	I	D	Y	L	L	L	S	N	W	V	P
P	D	L	T	D	E	S	L	A	S	Q	V	E	Y	L	L	L	N	G	W	V	P
P	D	L	T	T	E	S	L	A	S	E	V	E	Y	L	L	L	N	G	W	V	P
P	P	L	T	V	T	Q	L	A	K	E	V	D	Y	L	L	L	N	G	W	I	P
P	T	L	T	D	E	Q	L	L	K	E	I	D	Y	L	I	R	K	K	W	I	P

that we have sampled from the family that has a conventional N-terminus, the other ten species having the highly distinctive *Phe-Asn,* which alone accounts for three nucleotide differences.

Four Myrtalean families and Thymelaeaceae. In this study four families which, as discussed above, are agreed to be members of the order Myrtales, were chosen and, from each, two species, each from a different genus, were selected. Dahlgren and Thorne (1984) considered that, though closely related, Thymelaeaceae was not a Myrtalean family, so it was chosen as an "out-group" (to define the base of the tree) and two species were studied. When these ten species were analyzed simultaneously, there were two consensus trees out of 17 minimal trees (Fig. 2). In one tree the species pair perfectly into the five families, whereas in the other two species of Lythraceae lie side by side. Sequences at the five familial nodes shown in Figure 2 were derived and used in an analysis with *Ludwigia, Lopezia,* and *Circaea* and other external angiosperm nodes (see below) to give the familial node for Onagraceae shown in Figure 1. The grouping of the six familial nodes is shown, with other information, in Figure 3; five of the families arise from a single junction but Onagraceae diverge separately though close to the five. The surprising result in this tree is that Thymelaeaceae appear to be a very definite member of the same group as most of the Myrtalean families and not, as had been expected, an "out-group."

Euphorbiales. In one of the currently respected angiosperm taxonomies, Cronquist (1981) did indeed place Thymelaeaceae in Myrtales, although he did so because the family fits in there more easily than anywhere else, not because he considered it a clear-cut Myrtalean family (Cronquist, 1984). Dahlgren and Thorne (1984) stated that a number of taxonomists believe that Thymelaeaceae approach most closely Euphorbiales and they themselves considered that Thymelae-

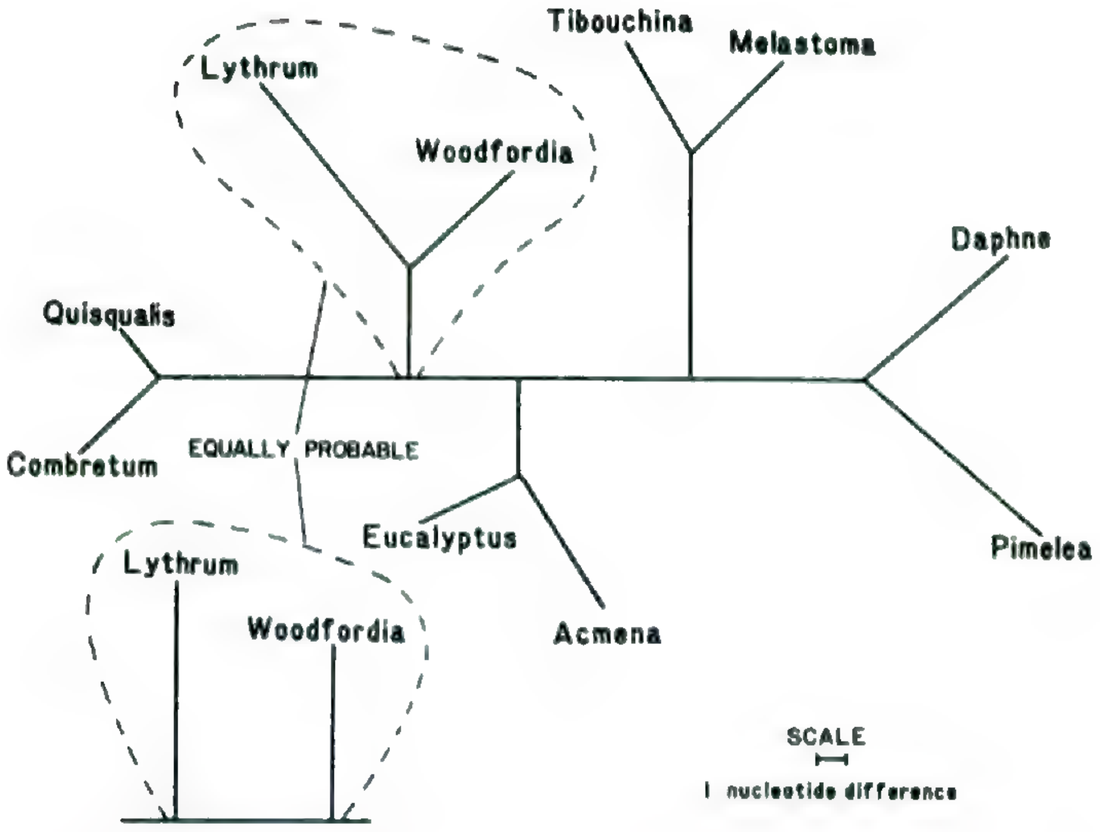

FIGURE 2. Unrooted phylogenetic tree for two species from each of five families. The members of a family pair perfectly in one consensus tree but in the equally probable second tree the two members of Lythraceae are side by side. For species names see Table 1. Note that in these trees angles are meaningless. Five of the familial nodes used in deriving Figure 3 were obtained from this tree.

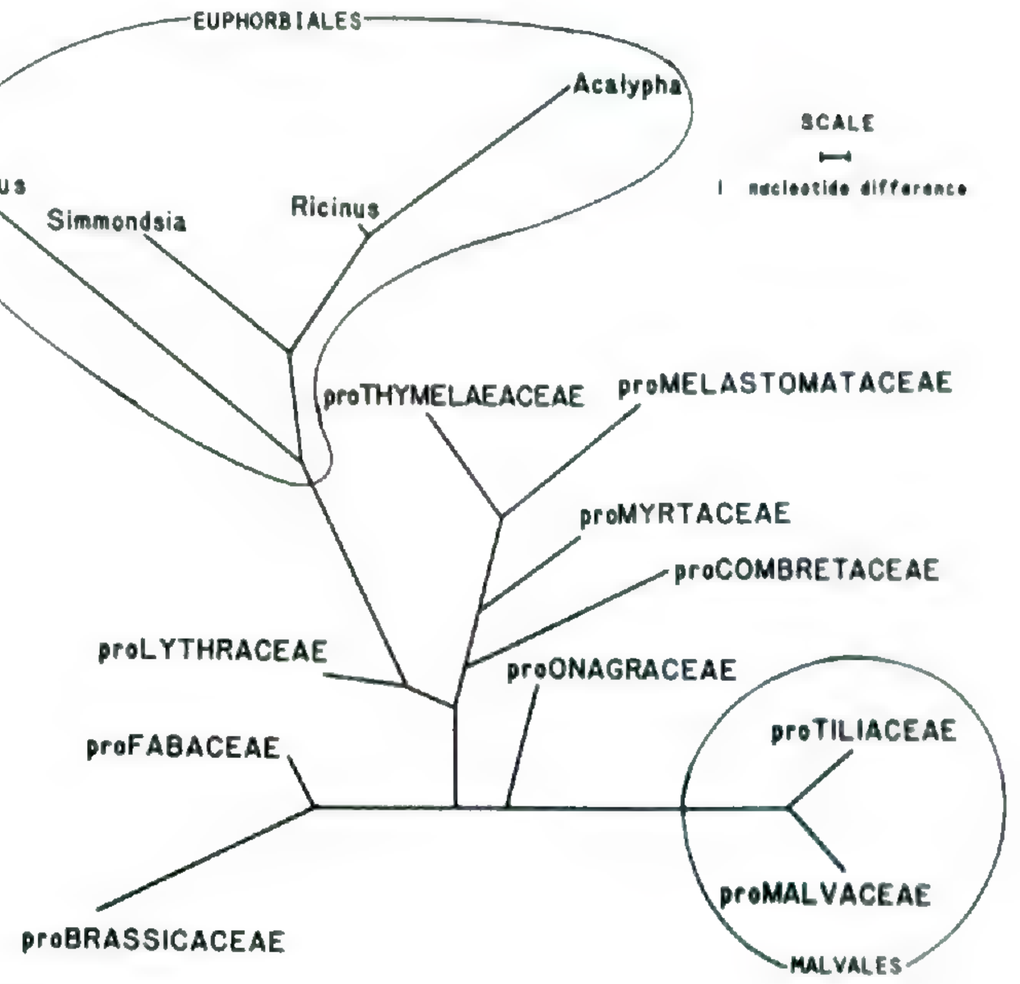

FIGURE 3. Unrooted minimal phylogenetic tree for ten familial nodes and four species from Euphorbiales. The familial nodes were derived from the analyses represented in Figures 1, 2, and 4.

aceae should be placed near Euphorbiaceae, and that these two families are related to Malvales. It therefore seemed appropriate to investigate Euphorbiales and Malvales.

To represent Euphorbiales, two species were chosen from Euphorbiaceae and two from Buxaceae, although it was understood that one of the latter, *Simmondsia,* is often placed in a family of its own. The four species were first analyzed in conjunction with the Myrtalean familial nodes mentioned above; all four diverged from a common node, confirming the reality of the order Euphorbiales with the two Euphorbiaceae appropriately grouped. However, the two putative Buxaceae did not have a common familial node suggesting that the separation of Buxaceae and Simmondsiaceae might indeed be valid.

In the Malvales, three species of Malvaceae had already been studied (Martin & Dowd, 1984) so, in order to broaden the representation, two species of Tiliaceae were sequenced. These were analyzed with the Malvaceae species and from the minimal tree (Fig. 4) both familial nodes were derived.

The analysis of the familial nodes for the five families of Myrtales, Thymelaeaceae, Euphorbiales, and Malvales was carried out with nodes for two other "external" families, Fabaceae and Brassicaceae (Martin et al., 1983) (Fig. 3). Thymelaeaceae do not move from their position in the Myrtales and Onagraceae still diverge slightly separate from most Myrtales. The major surprise is that Euphorbiales diverge from the Myrtalean tree. We have carried out similar analyses substituting other families for the two "external" ones without changing this result. Thus, except for the junction with the Euphorbiales and Thymelaeaceae, four of the Myrtalean families (Lythraceae, Combretaceae, Melastomataceae, and Myrtaceae) form a natural group as would be expected for an order like Myrtales.

DISCUSSION

As an exercise for testing the ability of objectively-generated phylogenies derived from sequence data to reflect the conclusions of taxonomy, this must be regarded as at least a partial success. Most notable is the correct grouping of species into families as displayed in Figures 2, 3, and 4. In the more extensive study of Onagraceae, two successes can be recorded; the correct grouping of two species each into the genera *Clarkia* and *Epilobium*; and the identification of the first divergence, which confirms several other lines of strong evidence that *Ludwigia* is the "sister group" of all other Onagraceae (Raven, 1979). The separation of the taxa into the other six tribes (Raven, 1979) is more uncertain and three of them (Onagreae, Hauyeae, and Epilobieae) depart from the tree so closely that they are effectively indistinguishable; according to Raven (1979) there is a possible relationship between Hauyeae and Onagreae. The other three tribes (Lopezieae, Circaeeae, and Fuchsieae), which are

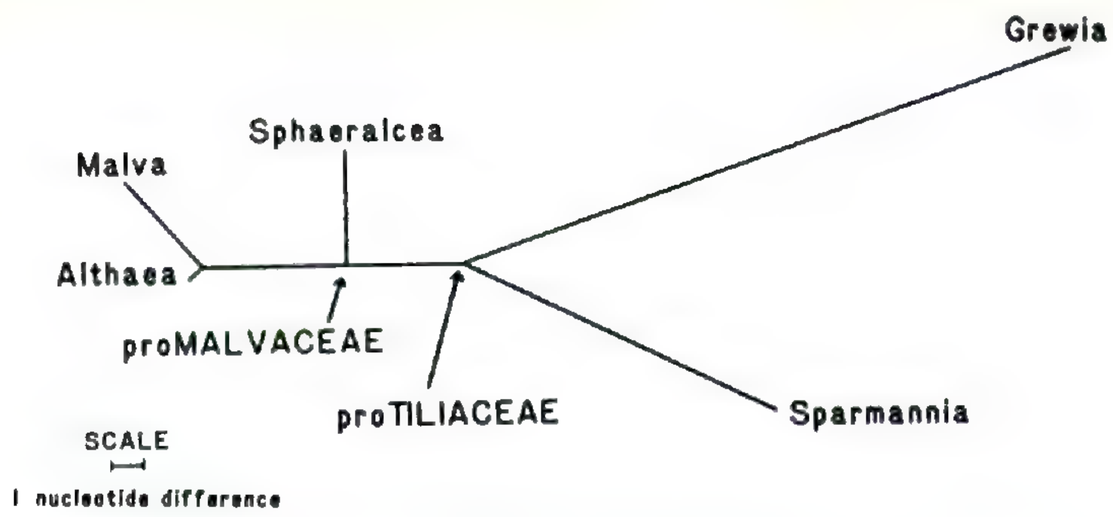

FIGURE 4. Unrooted minimal phylogenetic tree for species of Malvaceae and Tiliaceae. The familial nodes for these two families, used in Figure 3, were derived from this tree.

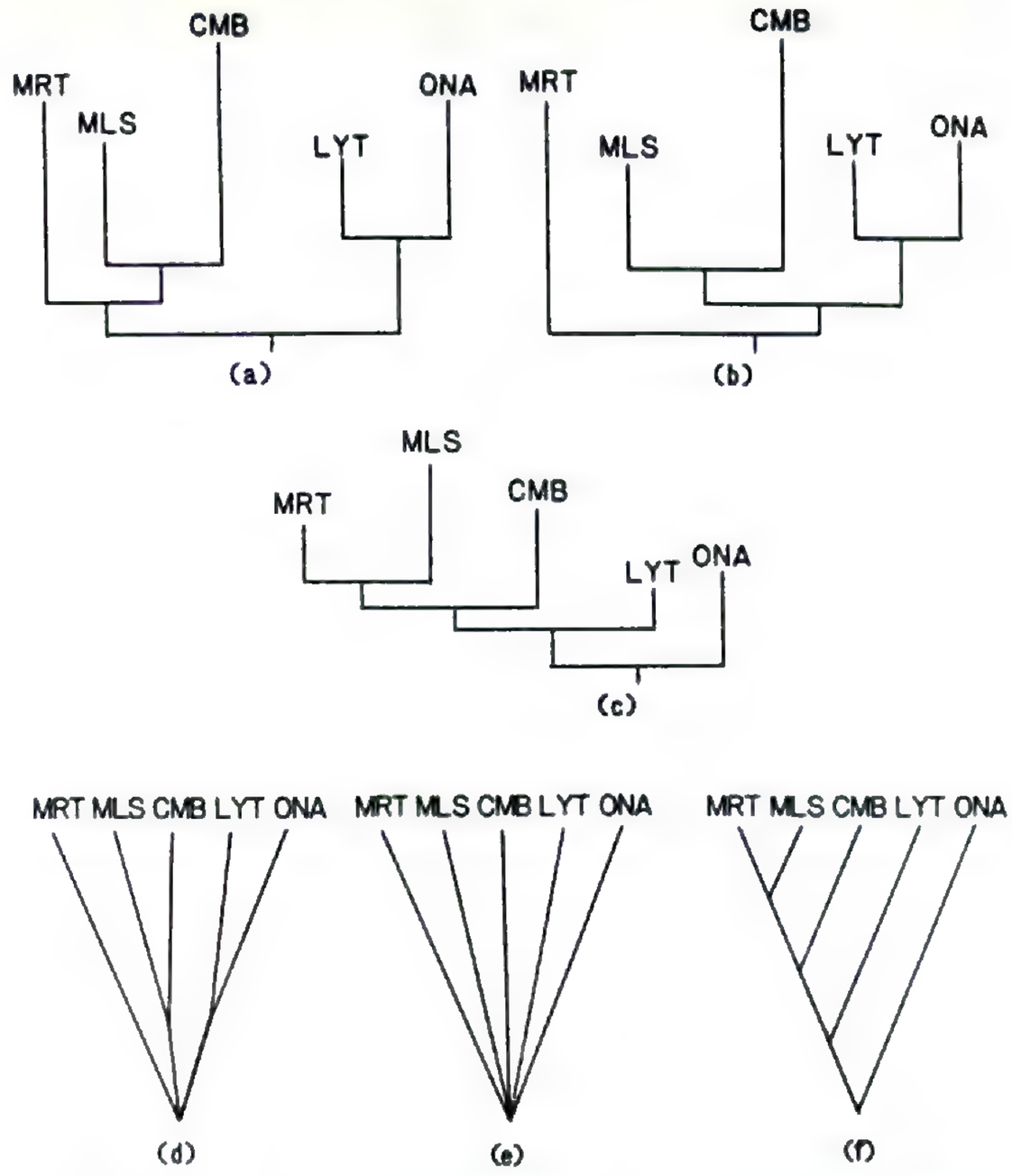

FIGURE 5. A comparison of phylogenies from Johnson and Briggs (1984) (a, b, d, and e) with equivalent ones from this paper (c and f). a and b are from Johnson and Briggs' phylograms A and C, respectively, and d and e are congruence cladograms (not to scale) from their figures 6 and 7. MRT, Myrtaceae; MLS, Melastomataceae; CMB, Combretaceae; LYT, Lythraceae; ONA, Onagraceae.

all monogeneric, are not confused but *Fuchsia* is thought to be the most generalized and might have been expected to diverge earliest. These are rather stringent tests of our methods because, when relationships are close and differences are small, chance is more likely to operate to give a misleading result; for this reason, Martin et al. (1983) made a strong point of deriving familial nodes from which to generate inter-familial phylogenies, the primary purpose of this research.

When considering the comparison of our phylogenetic trees with those derived for the Myrtales from taxonomy, the best source of comparison appears to be four trees derived from Johnson and Briggs (1984). These authors do not appear to have a clear preference for one or more of these so all are shown in Figure 5; only the families that overlap with this study are represented, viz. Onagraceae, Lythraceae, Combretaceae, Melastomataceae, and Myrtaceae. There appears to be enough variation present among these four trees to accommodate most of the differences in our tree. The main discrepancy is that in some of their trees Myrtaceae diverges near the base; the main similarity is that Onagraceae and Lythraceae usually diverge early. However, it must be said, without in any way implying criticism, that the main objective of the whole exercise has been partly frustrated by the lack of a clearly defined phylogeny to act as a model against which we can test our methods.

The inclusion of Thymelaeaceae as an "outgroup" for the Myrtales, as suggested by the paper of Dahlgren and Thorne (1984), did not serve that purpose because in our study the family grouped with Myrtales. This was indeed the opinion of Cronquist (1984), so we were able to perform a test, in the best scientific tradition, to distinguish between the hypothesis of Cronquist and the alternative one of Dahlgren and Thorne (1984), that of a relationship of Thymelaeaceae to Euphorbiales and Malvales. The results of our test supported Cronquist's hypothesis in that Thymelaeaceae did group with Myrtales, but this result should be considered in the light of the fact that there are sequence data for less than 15% of dicotyledonous families; given tests against a much wider range of variation, the family may well group elsewhere. We believe that the fact that Thymelaeaceae and Euphorbiales do not group with Malvales is stronger evidence against the hypothesis of Dahlgren and Thorne (1984).

In another respect the test has been partly successful because the families of Myrtales do form a natural group separate from others, always excepting Euphorbiales and, possibly, Thymelaeaceae. It is true that Onagraceae seem to diverge separately from the rest but additional data could conceivably change this. It must be acknowledged that Hutchinson (1973) placed Onagraceae in an order of their own but this seems to be quite contrary to the great majority of evidence produced in the symposium at the XIII International Botanical Congress (Raven, 1984).

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PALEOGENE PHYTOGEOGRAPHY AND CLIMATOLOGY OF SOUTH AMERICA[1]

EDGARDO J. ROMERO[2]

ABSTRACT

Paleogene, Maastrichtian, and Miocene floras are reviewed. They are located on continental margins, where several sedimentary basins developed. The affinities of the fossil genera to living ones allow the recognition of three paleofloras: Neotropical, Mixed, and Antarctic. These could be the forerunners, respectively, of the presently more humid dominions in Neotropical Region (Caribbean, Amazonic, and Guayano), of the drier ones (Chaqueño and Andino-Patagonico), and of the Subantarctic Dominion of the Antarctic Region. The South American climate, as indicated by the fossil floras, showed a trend to higher temperatures during the Paleocene and Lower Eocene, and a deterioration through the Middle and Upper Eocene.

The purpose of the present work is to review the Paleogene taphofloras of South America and to analyze their paleophytogeographical and paleoclimatical significance.

This problem has interested botanists and paleontologists in the past. Berry (1921, 1938, 1940) published several reviews as a direct result of his work in the continent. More recently, Menéndez (1964, 1969, 1971) detailed the taphofloras and the areas occupied by the different types of vegetation, and Volkheimer (1971) gathered evidence about the paleoclimatology of Argentina. Later, Archangelsky and Romero (1974) analyzed the environmental conditions based on the pollen record of the southern South American Paleogene, and Aragón and Romero (1984), Romero (1978), Romero and Arguijo (1981b, 1982), and Romero and Dibbern (1984) analyzed some taphofloras of the same region. Therefore, much new geological, botanical, and paleontological evidence has been gathered, warranting a new review.

The present paper is arranged in two parts. The first one reviews every published outcrop with impressions known to the author from the Paleogene of South America, complemented with information about fruit casts, petrified wood, and palynology. Data about some Maastrichtian and Miocene floras have been added to show more general trends in the changes. The age of the deposits was updated according to recent publications. The second part discusses the phytogeographical areas that could have existed during that time, and the climate under which they have developed.

There is not an agreement on the terminology to be used in biogeographical discussions, especially among paleobotanists. I shall use a few of them, in an attempt to reach more accuracy and clarity, but without discussing their antecedents or convenience, which surpasses the limits of the present paper. They are:

Flora. The list of the plants living together in a given area at a given moment. They may be fossil or living.

Vegetation. Plant cover in a given area at a given moment, fossil or living. Their association, ecology, and life forms, rather than their taxonomic identity, are considered.

Taphoflora. The list of the fossil plants preserved in a given outcrop. They represent the original flora, as affected by dispersal, burial in that place, diagenesis, and differential alteration. They are the smallest real evidence to be used in paleophytogeography.

Paleoflora. A fossil flora that may be characterized by its systematic list, and so differentiated from other fossil floras. Each paleoflora may comprise several taphofloras. From the characteristic systematic list a characteristic plant association may be hypothesized, and so vegetational features suggested.

A REVIEW OF THE PALEOGENE TAPHOFLORAS OF SOUTH AMERICA

Figure 1 shows the positions of the known Paleogene taphofloras, and some Late Cretaceous and Early Neogene ones. They are located on the margins of several marine basins that existed

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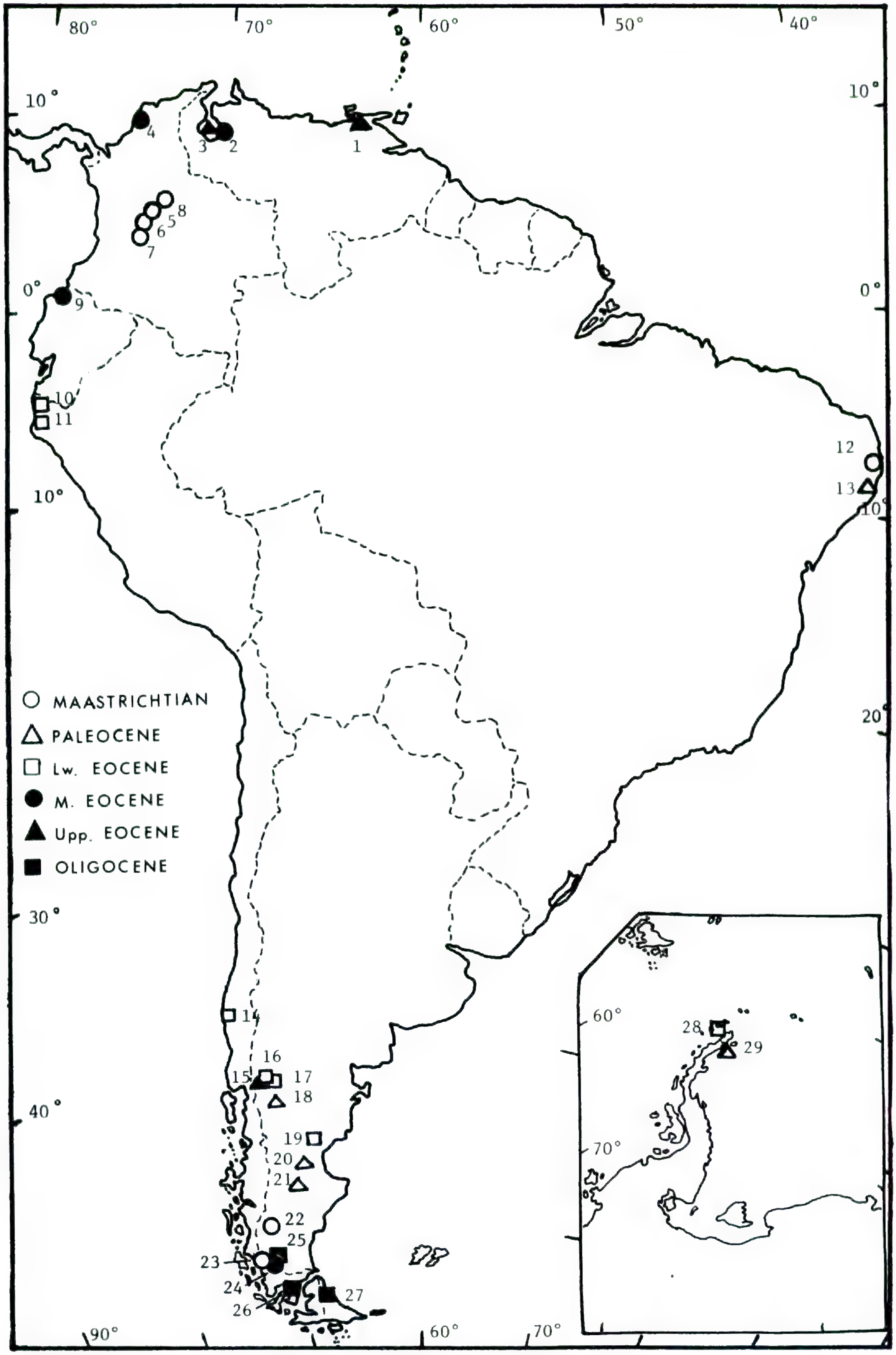
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Upp. EOCENE
OLIGOCENE

during the Upper Cretaceous and Lower Tertiary (Fig. 2). These basins are related to similar ones of the Upper Cretaceous and the Oligocene-Miocene (Bertels, 1979; Zambrano, 1981), which changed considerably the configuration of the continent. Most of the fossil floras have been buried in deltas, coastal swamps, or lagoons.

MAASTRICHTIAN

Included here are the outcrops of the Gauduas Formation in the vicinity of Bogotá, Colombia, originally described as Miocene, but they correspond to the Maastrichtian according to van der Hammen (1954). These outcrops are located in Cipacón (Fig. 1.6) and Zipaquina (Fig. 1.7) (Department of Cundinamarca), El Infierno (Fig. 1.5) (Department of Boyacá), and Falls of Tequendama (Fig. 1.8) near Bogotá. Fruit casts and leaf imprints have been described: among the former, *Humiria cipaconessis* (Berry, 1924a; Selling, 1945); among the latter, *Geonomites zipaquinensis, Ficus andrewsi, Coussapoa camargoi, C. ampla, Nectandra lanceolata,* and *Theobroma fossilium* (Berry, 1929a; Huertas, 1960). *Humiria* was also found in Belén, Perú (Lower Eocene) (Berry, 1927, see below). The palynological record shows that northern South América was a province rich in American elements, where palms dominated (van der Hammen, 1954).

In Brazil, *Palmocarpon luisi* is quoted in the Paraíba Group (Fig. 1.12) in Paraíba state (Maury, 1936).

In southernmost South America, the taphoflora of Cerro Guido (Fig. 1.23) has approximately 30 species of leaf imprints, most of which have been attributed to Lower Cretaceous species of North America. They have been studied by Kurtz (1899), with a few additions by Hunicken (1971), and Menéndez (1966, 1972a, 1972b). Many have palmatilobate leaves.

The deposits of the Mata Amarilla Formation, though of Coniacian age (earlier than the Maastrichtian) (Romero, 1978), are also worth mentioning because they present some species that migrated to Australasia during the Paleogene. Among them, some have or have had a cosmopolitan distribution (*Hymenophyllum, Podocarpus*), but others are mainly southern (*Dacrydium, Gleichenia*). Some extended as far as New Zealand (*Blechnum, Laurelia*) during the Tertiary.

Fossil leaves of *Nothofagus* have not yet been found in the South American Maastrichtian, but a few pollen grains have been found, already differentiated into three types (*fusca, brassi,* and *menziesii*) in sites some 1,500 km apart (Archangelsky & Romero, 1974; Romero, 1973). The site of the plants that produced these pollen grains has not yet been discovered.

PALEOCENE

Paleocene taphofloras are not known in northern South America, but the palynological evidence (Muller, 1970, 1981) already indicates the presence of Bombacaceae (*Bombax* type). In northeast Brazil (Fig. 1.13), fruits of *Nypa pernanmbucensis* and *Celtis santosi* and imprints of *Psidium* have been found (Beurlen & Sommer, 1954; Dolianiti, 1955).

In southern South America the oldest Tertiary deposit is that of Funes (Fig. 1.20) of Danian age (Berry, 1937a; Romero, 1978), probably together with that of Sur del Río Deseado (Fig. 1.21) (Arguijo & Romero, 1981; Hunicken, 1968; Spegazzini, 1924). In these, 11 and three species have been discovered respectively, of which only one is found in other deposits. All the species seem to belong to subtropical genera of the Neotropical Region.

The information on these taphofloras may be complemented with the results of palynological (Archangelsky, 1973, 1976a, 1976b) and paleoxylological studies (Petriella, 1972), which culminated with a paleoenvironmental reconstruction (Petriella & Archangelsky, 1975). This

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FIGURE 1. Paleogene taphofloras of South America.—1. Santa Bárbara, Trujillo Venezuela.—2. Escuque, Venezuela.—3. Maracaibo, Venezuela.—4. Dpto. Bolivar, Colombia.—5. El Infierno, Boyacá, Colombia.—6. Cipacón, Cundinamarca, Colombia.—7. Zipequina, Cundinamarca, Colombia.—8. Tenquendama, Colombia.—9. Ancon, Ecudador.—10. Sur de Talara, Perú.—11. Belén, Perú.—12. Paraiba, Brasil.—13. Pernambúco, Brasil.—14. Lota y Coronel, Chile.—15. Ñirihuau, Argentina.—16. Río Pichileufú, Argentina.—17. Río Chenqueniyen, Argentina.—18. Laguna del Hunco, Argentina.—19. Cañadón Hondo, Argentina.—20. Funes, Argentina.—21. Sur del Río Deseado, Argentina.—22. Mata Amarilla, Argentina.—23. Co Guido, Chile.—24. Río Turbio, Argentina.—25. Río Guillermo, Argentina.—26. Loreto, Chile.—27. Río Leona, Argentina.—28. Ia 25 de Mayo, Argentina.—29. Ia Seymour, Argentina.

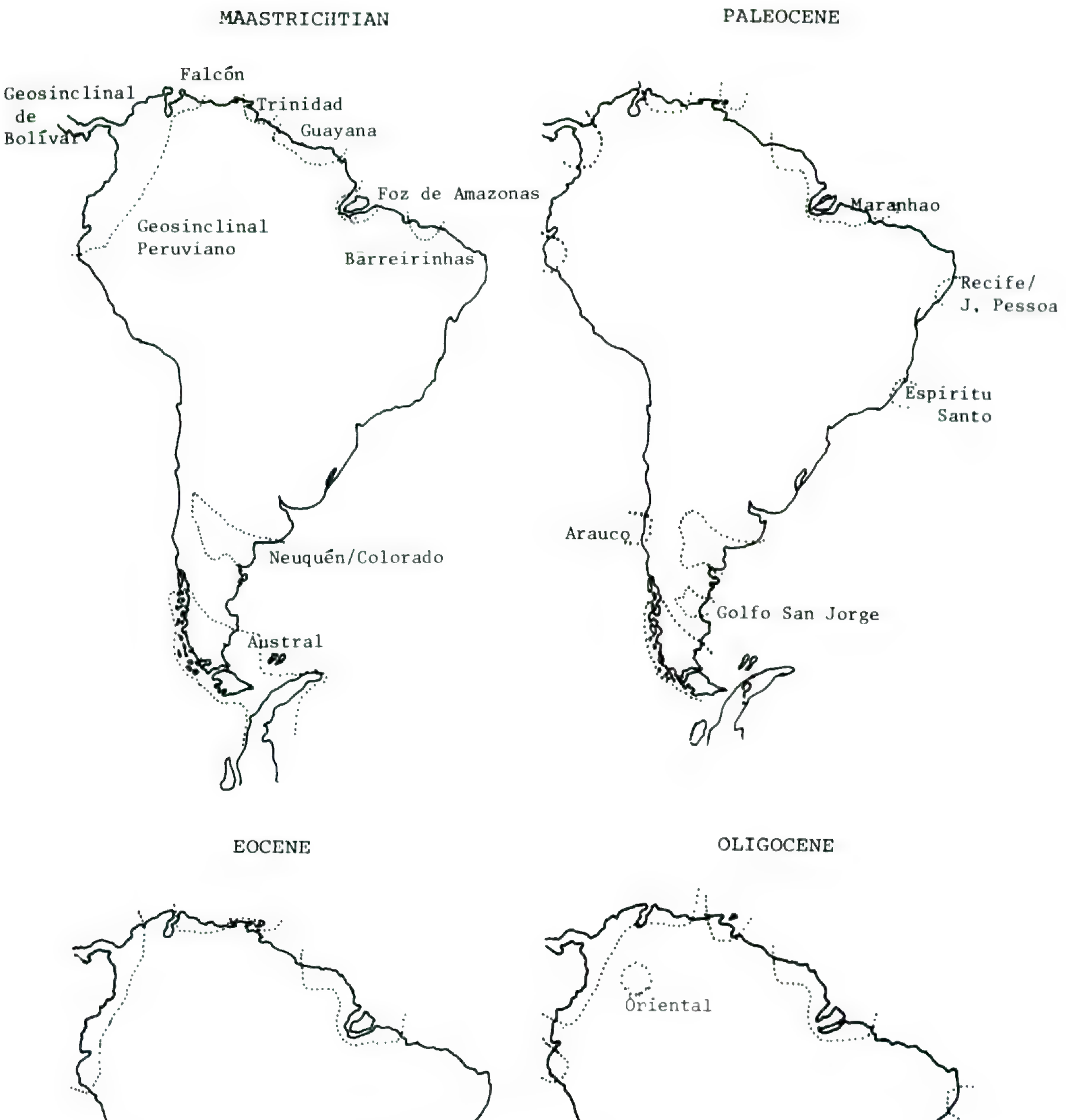

FIGURE 2. Marine basins in South America. From Bertels (1979), slightly modified.

reconstruction showed in the region of Golfo San Jorge (latitude 46°S) a vegetation section similar to the one found today in southern Brazil, some 2,000 km and 20° further north. It includes mangrove communities, swamp forest, tropical rain forest, mountain rain forest, highland forest, and sclerophyllous forest or savanna. The climate must have been subtropical humid. This coincides with the findings of crocodiles, which indicate that the 10° July isotherm passed through the region at that time, whereas at present it is some 1,500 km further north (Volkheimer, 1971).

Among the genera that constituted these communities, several were of Australasian origin such as *Dacrycarpus, Dicranopteris,* and *Gunnera,* and *Tricolpites fillii,* similar to *Beauprea,* which existed in New Zealand during the Cretaceous. Other elements appear simultaneously in New Zealand and South America, such as *Anacolosa* and *Nypa,* although they were not as frequent in South America as in Australasia. *Nypa* must have had a wide distribution because it has also been found in Pernambuco (Brazil) in Paleocene deposits. Other genera appear in these sediments for the first time, reaching New Zealand during the Eocene and Oligocene (*Retidiporites camachoi,* having affinities with *Banksia, Weinmannioxylon,* etc.).

The taphoflora of Laguna del Hunco (Fig. 1.18), in northwest Patagonia, is at least 59 million years old, as established by isotope dating (Archangelsky, 1974). It has some 25 described species (Berry, 1925), to which Petersen (1946) added a list of over 70 determinations. It has 69% of entire margined leaves. This percentage corresponds to the Paratropical Rain Forest according to Wolfe (1971, table 1) and to the Tropical Seasonally Dry climatic zone according to Dilcher (1973a, fig. 4). This taphoflora includes several genera of the present Neotropical Region (*Annona, Cochlospermum*) and others of the present Antarctic Region (*Lomatia, Peumus*), although it does not contain *Nothofagus*. Furthermore, endemics to the present Australian Region (*Casuarina* and *Akania,* Frenguelli, 1943; Romero & Hickey, 1976) and subtropical genera of xeric type (*Schinopsis*) have also been found in this taphoflora.

At a latitude of some 22° and 2,000 km further south is the taphoflora of Seymour Island (Fig. 1.29) (Isla C. Marambio in Argentine maps; Dusen, 1907). Its age is probably equivalent to that of Laguna del Hunco, since it seems to belong to the Paleocene Cross Valley Formation, according to Elliot and Trautman (1982). Dusen described 25 species and 64 forms determined to genera, especially of Pteridophyta, and he was the first author to point out the existence of a mixture of "temperate species" with "species similar to those of southern Brazil" or "subtropical" (Dusen, 1907). This taphoflora is presently found at a latitude of 64°31'S. It has 42% of entire leaves, which corresponds to a Subtropical Forest (Wolfe, 1971, table 1) or to Warm Temperate, probably moist, climatic zone (Dilcher, 1973a, fig. 4).

LOWER EOCENE

In northern South America the Lower Eocene is represented in Peru by the deposits of Sur de Talara (Fig. 1.10) and Belén (Fig. 1.11). The former was described (Berry, 1929b) as belonging to "Restin Formation" but in fact it corresponds to the Chacras Formation (Hoffstetter, 1956; Bertels, 1979). Berry described some of the fruits he studied as *Attalea olsoni, Iriartites restinensis,* and *Carpolithus jathrophaformis.* The second deposit (Belén) lies in the Pariñas Sandstone of Lower Eocene age (Hoffstetter, 1956). From these Berry, (1927, 1937c) described 11 species, belonging to genera such as *Palmacarpon, Humuria, Sapindoides, Cupanoides,* and *Anacardium.* The climate was "humid, lowland tropical," according to Berry (1927).

The deposits of Lota and Coronel (Fig. 1.14) in Chile are at a latitude of 37°S. Their age is Lower Eocene, although some authors consider it to be Paleocene (Palma Heldt, 1980). Engelhart (1891, 1905) and Berry (1922) described over 100 species, all of them assigned to Neotropical genera.

Berry expressed the opinion that "its elements are represented by modern species of tropical South America east of the Andes, and in the main of forms dwelling in the Amazon basin, especially toward the Peruvian part of the basin, and extending southward into eastern Bolivia . . . I would estimate the Chilean fossil flora as indicating a change from the present climatic conditions corresponding to from 10° to 12° of latitude at sea level." About the climate he said that "there was never frost" and it was "very much warmer and with more sunshine than at the present time." The percentage of species with entire margined leaves (70%) would indicate that it was a Paratropical Forest, in the sense of Wolfe (1971) or a Tropical, Seasonally Dry climatic zone in the sense of Dilcher (1973a).

In northwest Patagonia, the Lower Eocene is represented by two important deposits: Río Pichileufú (Fig. 1.16) and Río Chenqueniyeu (Fig. 1.17). Three species described from the outcrop of Alto Río Ñirihuau (Fiori, 1939) may be considered with the last one. All are thought to belong to the Ventana Formation (Aragón & Romero, 1984). They include some 140 species and 40 species respectively (Berry, 1938; Fiori, 1940) with a mixture of Neotropical and Antarctic elements. The first of these deposits is essentially similar to that of Laguna del Hunco, described above, and its percentage of entire-margined leaves is 69%. Berry (1938) pointed out the presence of genera that are a) tropical or subtropical, b) temperate, c) of semiarid environments (*Cupania, Schinopsis,* and *Schinus*), d) "from the temperate rain forest region of southern Chile," and e) 14 genera of possible lianas. The conditions were of humid and warm climate, judging from the flora, but the mixtures of elements did not allow Berry to classify them with certainty.

The taphoflora of Río Chenqueniyeu is also mixed, and very similar to the previous one, but it does include *Nothofagus.*

Somewhat further south, in the Basin of Golfo San Jorge, lie the deposits of Cañadon Hondo (Fig. 1.17), of which Berry (1932a) studied several small taphofloras. Their age is considered to be Eocene according to Andreis (1978) and they contain Neotropical and Subantarctic elements (see Romero, 1978, for a discussion of unpublished material).

Finally, some 2,000 km to the south, leaf imprints also are found (Orlando, 1963) in the taphoflora of Isla 25 de Mayo (King George) (Fig. 1.28) of the Antarctic Peninsula, at a latitude of 64°S. It contains Antarctic elements such as *Laurelia* and *Nothofagus,* but together with Neotropical ones such as *Schinopsis* and *Nectandra.* It may be especially compared with the taphoflora of Río Pichileufú. The total number of described species is only ten, but seven are entire margined. Although the number of species is not sufficient for a statistical analysis, it seems evident that the association was not less warm than subtropical. The age, given originally as Miocene, is considered to be Lower Eocene (Arguijo & Romero, 1981; Romero, 1978).

MIDDLE EOCENE

In the Department of Bolívar, Colombia (Fig. 1.4), Berry (1924b, 1929a) described several fossil fruits that he attributed to the Middle Eocene. These are *Sapindoides peruviana, Carpolithus bolivariensis,* and *Celtis bolivariensis.* In Venezuela near Escuque (Fig. 1.2), Berry (1920) discovered *Entada boweni,* of the Escuque Formation (Middle Eocene, Hoffstetter, 1937). In Ecuador, the area of Ancón (Fig. 1.9), Península de Santa Elena, yielded fruits of angiosperms (Berry, 1929c, 1932b). According to the collector (Sheppard, 1937) the fossils came from the Socorro Sandstone (Middle Eocene, Hoffstetter, 1936). The material includes *Astrocarym sheppardi, Ventanea sheppardi, Palmocarpon bravoi, Annona peruviana,* and *Sapindoides peruvianus.* The last three are also found in the deposit of Belén, and the last is also found in the Department of Bolívar, Colombia. The genera belong to a Neotropical lineage, and the environment that they indicate is a lowland rain forest.

In Patagonia, the fossil floras of the Middle Eocene are represented in the Río Turbio Formation (Fig. 1.24). This important formation contains several levels with imprints, which were studied by Berry (1937b), Frenguelli (1940), and Hunicken (1955, 1967). The levels "s" and "t," which were studied specially by the last author, contain a mixture of Neotropical and Antarctic genera, including *Nothofagus.* The pollen analysis indicated that in several levels the pollen grains of *Nothofagus* may be dominant (Archangelsky & Romero, 1974; Romero, 1977). The percentage of entire-leaved species is 40%, which would indicate a Subtropical Rain Forest (Wolfe, 1971) or a Warm Temperature, moist, climatic zone (Dilcher, 1973a).

UPPER EOCENE

The Upper Eocene is represented in Venezuela, near Santa Bárbara (Fig. 1.1), Zulia State (Berry, 1936), and in the basin of Maracaibo (Fig. 1.3) (Berry, 1939). Berry described leaf imprints of nine species already known in, or linked to, the floras of the Coastal Plain of North America. They belong to the genera *Apocynophyllum, Burserites, Cedrela, Chrysophyllum, Ficus, Inga, Terminalia,* and *Combretum,* suggesting the extension "of an equable and warmer climate north of the equatorial zone."

In northwest Patagonia, approximately at the latitude at which paratropical rain forest developed during the Lower Eocene, several outcrops with leaf imprints were found in the Ñirihuau Formation (Fig. 1.15) (Aragón & Romero, 1984; Berry, 1928; Feruglio, 1941; Fiori, 1931, 1939; Romero & Arguijo 1981a). Altogether these out-

crops have yielded some 45 species of Antarctic genera. They are strongly dominated by genera such as *Nothofagus, Araucaria,* and *Lomatites.* The percentage of species with entire margin decreases to 27% representing a Mixed Mesophytic Forest according to Wolfe (1971) and Cool Temperature, moist, climate zone according to Dilcher (1973a).

OLIGOCENE

No confirmed records of Oligocene plants are known to me from northern South America. Some deposits attributed to that age are actually older, such as that of Pariñas Sandstone in Belén, Perú, or that of Falls of Tequendama, Colombia, mentioned above.

In the southern extreme of the continent there are plant imprints in several taphofloras of the Río Guillermo (Fig. 1.25), Río Leona (Fig. 1.27), and Loreto Formations (Fig. 1.26) (Dusen, 1899; Frenguelli, 1940; Gilkinet, 1912; Hunicken, 1955). The first of these lies unconformable on the Río Turbio Formation mentioned above, and its age was established as Oligocene-Miocene by Hunicken (1955). The Río Leona Formation is considered to be correlated with the lower section of the Río Guillermo Formation (Russo et al., 1980). The Loreto Formation is considered to be Upper Eocene or Oligocene (Fasola, 1969), slightly more modern than the Río Turbio Formation. Arguijo and Romero (1981) found that the fossils contained in these three formations are very similar (Jaccard index ca. 50). Consequently, it seems logical to consider the taphofloras of the three formations together, and attribute them for the moment to the earlier Oligocene, or perhaps to the later Eocene.

The leaf imprints represent 27 species of Fagaceae and associated plants of the Antarctic Region, although Dusen (1899) pointed out that the greatest affinities of the flora are with the associations presently limited to the northern extreme of the Subantarctic Province, some 1,000 km north of the fossiliferous outcrops. The percentage of entire margined leaves is similar to that of the Ñirihuau taphoflora, of the Upper Eocene, but the size of the leaves seems to be substantially smaller, generally nanophylls, or at the most microphylls.

MIOCENE

Outcrops of Miocene age with plants are abundant in South America and some of them are classical, such as those of Loja and Cuenca Basins (Ecuador), but their consideration lies outside the scope of the present work.

It is noteworthy that they are absent from Patagonia and the southern part of Chile. Thus they reflect a change in the deposition regimes as was pointed out by Yrigoyen (1969), and Pascual and Odreman Rivas (1971), based on different kinds of evidence. Furthermore, many of them that indicate humid, lowland tropical forest appear in present day highlands or desert areas, thus making it possible to establish, together with others of Pliocene and Pleistocene ages, the time at which the Andes started to rise, producing changes that lead to the formation of deserts and highland environments (Menéndez, 1971; Axelrod, 1979).

Discussion

PALEOPHYTOGEOGRAPHY

The living vegetation of South America belongs to two botanical Regions: Neotropical and Antarctic (Cabrera & Willink, 1973). The Neotropical Region covers most of the continent under an array of very variable climatic conditions. Wet forests comprise the Caribbean, Amazonian, and Guayanan Dominions; drier and poorer forests correspond to open areas without trees and comprise the Chaqueño and Andino-Patagonian Dominions. The Antarctic Region contains a wet to rather dry forest, in the only Subantarctic Dominion.

Figure 3 shows the taphofloras discussed in the previous section placed according to their age and approximately at their present latitudes. I used present latitudes because the plotted outcrops belong to different ages. Furthermore, the South American continent has not migrated very much since the Cretaceous. According to Valencio et al. (1971), in Cretaceous times it was about 10° more to the north, and a slow, uniform, nonrotating displacement has occurred since then.

Three main sectors may be observed in Figure 3. The first one at the upper left contains all the taphofloras with genera of the Neotropical Phytogeographic Region or their ancestors, exclusively. These taphofloras constitute the *Neotropical Paleoflora.* The second one, at the upper right, contains the taphofloras with genera characteristic of the Antarctic Phytogeographic Region, or their ancestors. This is the *Antarctic Paleoflora.* Between them, the third sector contains the floras that seem to present a mixture of species of both lineages. This is the *Mixed Paleoflora.*

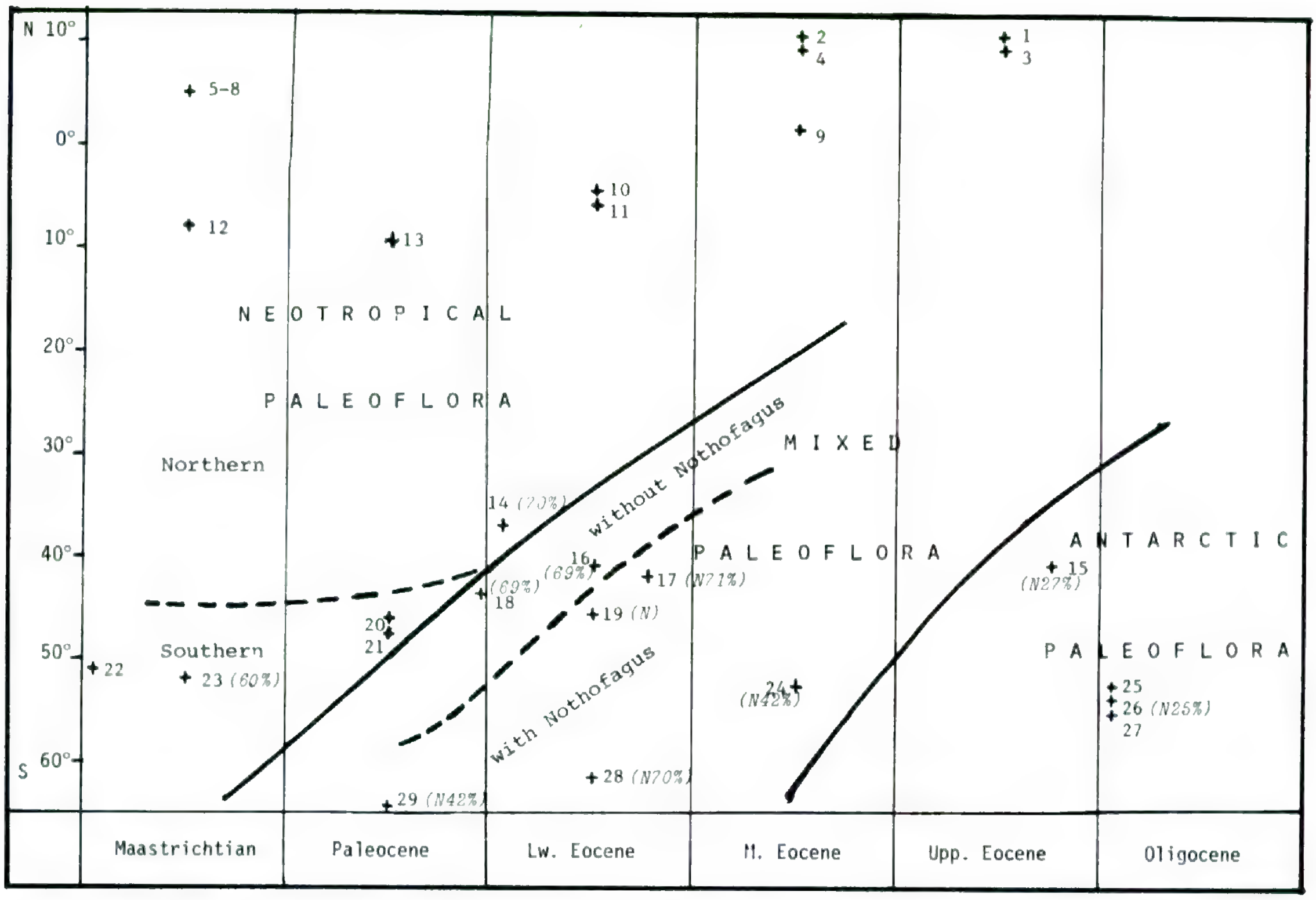

FIGURE 3. Age of Paleogene taphofloras of South America. See numbers in caption of Figure 1. Solid lines separate the paleofloras. Dashed lines separate probable provinces within them. Percentages of entire-margined leaves and the presence of *Nothofagus* (N) are denoted.

The neotropical taphofloras cover almost all South America during the entire period considered in this paper. The antarctic ones covered only the southern area from the Upper Eocene onward. The mixed ones covered almost all of Patagonia to the Antarctic between the Upper Paleocene and the Middle Eocene.

According to Dusen (1899), mixed floras were explained by an altitudinal zoning of the species, where those belonging to the Antarctic Region occupied the uplands, and those of the Neotropical Region the lowlands. I (1978) suggested that these taphofloras constituted the remainders of a stable phytogeographical unit with definite characteristics and particular ecological requirements, without strict equivalence with present plant formations, which I called *Mixed Paleoflora.*

Coincidentally, Dilcher (1973a) pointed out that in the past, both Asa Gray and R. W. Brown added genera that they considered temperate to the floras of Kentucky and Tennessee. But rather than mix these temperate forms in to so-called subtropical coastal flora, they postulated their source area in the Appalachian uplands. At present, several authors have ceased to consider those floras subtropical, and Dilcher is of the opinion that they were "probably temperate forms present in the lowland community which we would not recognize as elements of a lowland flora today."

Also, Kemp (1978) found that, in Australian Eocene outcrops known palynologically, there is an "anamalous mixture of tropical or subtropical rainforest types with those of cool temperate rainforest communities . . . (which) . . . suggests that the early Tertiary vegetation cannot be represented by a single modern forest type. It may be that the climate regime which supported this forest has no modern analog."

I suggested earlier (Romero, 1978) that the *Mixed Paleoflora* would be characterized by a mixture of genera from other units, whose species would have had, however, ecological requirements different from the living species of the same genera, and by genera of its own, linked with the present Chaqueño Dominion. I espe-

Species	Paleoflora: Upper Cretaceous	Lower Tertiary: Antarctic		Lower Tertiary: Mixed						Neotropical
	22	26	25	16	18	24	28	19	17	
Schinopsis sp.	*									
Schinopsis										
patagonica					*		*			
balansiformis				*	*					
moronghifolia				*						
sp. 1						*				
sp. 2										*
cf. *Schinopsis*										
Schinus molliformis				*						
Anacardites										
pichileufuensis				*						
brittoni				*						
patagonicus										*
sp.						*				
Astronium argentinum				*	*					
Roophyllum										
serratum		*				*				
nordenskjoldi	*							*		

FIGURE 4. Evolution of Anacardiaceae in southern South América from Cretaceous to Paleogene, from Romero (1978). See numbers in caption of Figure 1.

cially emphasized the evolution of the Anacardiaceae family in Patagonia, which, with only one species in the Coniacian (Upper Cretaceous), radiated during the Lower Tertiary, having five genera and 14 species in taphofloras of the *Mixed Paleoflora* (Fig. 4). Among those genera are *Schinopsis, Schinus,* and *Astronium,* which are conspicuous today in the Chaco, Caatinga, and Monte Provinces (Cabrera & Willink, 1973).

In the *Neotropical Paleoflora* a few taphofloras present elements now endemic to the Australian Region as discussed above. Upon this basis, it is possible to separate a northern, purely American Province, from a southern one, subject to migration (Fig. 3). In the *Mixed Paleoflora,* the absence of *Nothofagus* from taphofloras in Figure 3.16, 3.18, allows the separation of two provinces. Another separation is tempting, isolating taphofloras in Figures 3.24, 3.29, on the basis of their low percentage of entire-leaved species. However this is a physiognomic characteristic, and phytogeographic limits are being established in this paper on a floristic basis.

I therefore tentatively suggest that the *Neotropical Paleoflora* developed during the Lower Tertiary and was the forerunner of the more humid Dominions of the Neotropical Region (Caribbean, Amazonian, and Guayanan); that the *Mixed Paleoflora,* from the Upper Paleocene onward, gave origin to the drier Dominions (Chaqueño and Andino-Patagonian), and that the *Antarctic Paleoflora,* since the Upper Eocene, was the antecedent in South America of the Antarctic Region, represented today only by the Subantarctic Dominion. The real significance of further differences within the paleofloras is not yet apparent.

CLIMATIC CHANGES

Figure 3 shows the taphofloras discussed above and the corresponding paleofloras. The presence of *Nothofagus* was also denoted in several of them. Furthermore, the percentage of entire-leaved species was added in other cases. The merits of this last feature has been discussed by Dolph (1979), Dilcher (1973a), and Wolfe (1971, 1979) but ever since the observations of Bailey and Sinnot (1916), the high percentage has been considered a good indication of warm environment.

The areas covered by the different climatic types circumscribed on the basis of percentages of entire-margined leaves in South America do not coincide with the phytogeographical limits

of the *Neotropical, Mixed*, and *Antarctic Paleofloras*, as here defined. As an example, warm climates indicated by high percentages are present in both Provinces of the *Neotropical Paleoflora* and both Provinces of the *Mixed Paleoflora*. This is in accordance with the climatic variations within present Phytogeographic Regions (the Neotropical Region extends from the Amazonian wet warm forest to the Patagonian dry cold steppe) today and reflects the criteria used in this paper, whereas the Phytogeographic Regions were defined, as the recent ones are, on a taxonomic basis, and the climatic types were defined on a physiognomic basis.

The physiognomic analysis is relevant in this paper only for those taphofloras of Patagonia, because the rest, from northern South America, contain too few species for statistical analysis (Wolfe, 1975). The percentages used are mostly those given by Volkheimer (1971).

As shown in Figure 3, for the Maastrichtian, the taphoflora of Cerro Guido (Fig. 3.23) in southwest Patagonia, has 60% of species with entire-margined leaves.

For the Paleocene and early Eocene there are records in northwest Patagonia (taphofloras in Fig. 3.14, 3.16, 3.17) of 70% with entire-margined leaves. In the Antarctic peninsula there is an increase from 43% (Paleocene, Fig. 3.29) to about 70% (early Eocene, Fig. 1.28). Finally, during the late Paleocene, eastern Patagonia had a subtropical humid climate, with mangroves, crocodiles, etc., as explained above. Therefore, it may be accepted that since Maastrichtian to lower Eocene times a progressive temperature increase occurred.

For the Middle Eocene there is only a record in the Río Turbio taphoflora (Fig. 3.24), southwestern Patagonia, with a decrease up to 49% of entire-margined leaves. For the upper Eocene the Ñirihuau taphofloras (Fig. 3.15) in northwest Patagonia show a further decrease to 17%. And during the Oligocene, again in southwest Patagonia, the same percentage remains, with a dominance of small-sized leaves. Therefore, a deterioration of climate since Middle Eocene to Oligocene may be supposed.

Roughly speaking, the sequence of floras in Patagonia would imply variations from the equivalents of a Paratropical Rain Forest (Lower Eocene) to a Subtropical Forest (Middle Eocene), then to the Mixed Mesophytic Forest (Upper Eocene), and finally to a Mixed Northern Hardwood Forest (Oligocene) (sensu Wolfe, 1971).

In other parts of the world, a progressive temperature increase was detected during the Paleocene and Lower Eocene (Wolfe, 1978), although "cool intervals occurred during the late Paleocene, the late early to early Middle Eocene and the early Late Eocene" (Wolfe, 1978). The most important increase, during the late Eocene, is correlated with the Bertonian, although its "duration and exact timing is unknown" (Wolfe, 1975: 50). This brief shift was called the Eocene Terminal Event.

Finally, a major shift during the Oligocene was recorded in Europe, western Siberia, New Zealand, and western North America (Wolfe, 1971). It was more marked during the middle Oligocene and produced a spectacular transformation in the high latitude floras, which changed from having high percentages of large, evergreen broad leaves with entire margins to high percentages of dentate, small, deciduous leaves.

The data from South America are not abundant enough to show minute changes during the late Paleocene to the early late Eocene. However, a coincidence with the general trends to higher temperatures in other continents may be detected during the Paleocene and Lower Eocene, and then a deterioration through the Middle and Upper Eocene. The subsequent major shift during the Oligocene, however, is not yet apparent in this continent.

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NEW TAXA OF *CALADIUM, CHLOROSPATHA,* AND *XANTHOSOMA* (ARACEAE: COLOCASIOIDEAE) FROM SOUTHERN CENTRAL AMERICA AND NORTHWESTERN COLOMBIA[1]

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ABSTRACT

Six new infrageneric taxa of Araceae, subfamily Colocasioideae, are described. *Chlorospatha hammeliana* is described from a restricted area of Panama, *C. croatiana* ssp. *croatiana* from Costa Rica and Panama, and *Caladium lindenii* (André) Madison var. *sylvestre* from Panama and Colombia. These represent the first reported indigenous occurrences of the genera *Caladium* and *Chlorospatha* outside of South America. In addition, *Chlorospatha gentryi* and *C. croatiana* ssp. *enneaphylla* are described from northwestern Colombia. *Chlorospatha croatiana* and *C. gentryi* are the fourth and fifth species of their genus known to have compound leaves; a key is provided to all five. A brief review of generic distinctions within the tribe Caladieae precedes the description of the second known peltate-leaved species of *Xanthosoma, X. caladioides,* from eastern Panama.

The tribe Caladieae (sensu Madison, 1981), belonging to the subfamily Colocasioideae of the overwhelmingly tropical family Araceae, consists of six genera and 70–75 species, all confined to the New World. Three of the genera, *Aphyllarum, Jasarum,* and *Scaphispatha,* are monotypic and of restricted distribution in South America and will not be considered further in this paper. The remaining three genera, *Caladium, Chlorospatha,* and *Xanthosoma,* comprise the bulk of the species and range more widely, though only *Xanthosoma* has been heretofore reported to extend beyond South America (Croat, 1979; Madison, 1981).

The Caladieae appear to be especially diverse in the Andean regions of northern South America, and recent work on newly available collections from that area (Madison, 1981) has led to the clarification of generic concepts in the group. These refined concepts have, in turn, facilitated the placement of new taxa collected in South America and other regions, including those described below.

CALADIUM

Caladium lindenii (André) Madison is well known in cultivation as an ornamental plant with whitish or silvery leaf venation. This species is more commonly, but improperly, known as *Xanthosoma lindenii* (André) Engl., the transfer to *Caladium* having been made only recently (Madison, 1981). It was first described, as *Phyllotaenium lindenii* André, in 1872, from plants supposedly collected in Colombia; although persisting in cultivation, the species was not found again in the wild until 1939, when a form with plain green leaves was collected in Chocó Department, Colombia (*Killip 35140,* COL). Subsequent collections have extended the known natural range of this species—and consequently of the genus *Caladium*—into central Panama. All collections of the plain-leaved form have, until recently, either been misidentified or left undetermined.

The "wild type," plain green-leaved form of *Caladium lindenii* is described below as a new variety.

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[1] I am grateful to Thomas B. Croat for assistance in my work at the Missouri Botanical Garden and for providing the photographs of *Chlorospatha croatiana* and *C. hammeliana.* I also thank Alwyn H. Gentry for allowing me to use his photo of *C. gentryi.* Barry E. Hammel supplied fresh pollen samples from the field, in addition to herbarium specimens, and Frances Mazanec critically reviewed and rewrote the Latin diagnoses for all taxa except *Xanthosoma caladioides*; to both of these individuals I am deeply appreciative. The investigation of pollen morphology in *Caladium lindenii, Chlorospatha croatiana,* and *Chlorospatha hammeliana* was facilitated by National Science Foundation grants to James W. Walker as well as an Albert DeLisle Scholarship (University of Massachusetts) to the author.

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Caladium lindenii (André) Madison var. **sylvestre** Grayum, var. nov. TYPE: Panama. Panamá: El Llano–Cartí Rd., 9 mi. from turnoff of PanAmerican Hwy., ca. 300 m, *Hammel et al. 11341* (holotype, MO-2982267).

Var. *sylvestre* typico immaculatis viridis laminis distinguenda. Lamina simplex, sagittata, inferiore pagina minute ferrugineo-furfuracea; petiolus 40–95 cm longus, ferrugineo-furfuraceus; lobus anticus 25–35 cm longus, 15–25 cm latus; lobus posticus 9–18 cm longus. Inflorescentia solitaria; pedunculus 6–17 cm longus; spatha 8–12 cm longa; tubus 4–5 cm longus; spathae lamina 5–8 cm longa; spadix pars mascula 4–4.5 cm longa.

Terrestrial herb, ca. 75 cm tall. Stem ca. 2–2.5 cm diam. (*Croat 52023, 56094*), largely or entirely subterranean. Petiole purplish at the base, "narrowly flattened" (*Croat & Cagallo 52150*) to "narrowly and obtusely sulcate" (*Croat 56094*) adaxially, with scant milky sap or sap not evident at all, 40–95 cm long, covered with sparse, tangled, reddish brown scurf. Lamina sagittate, not peltate, the anterior lobe 25–35 cm long, 15–25 cm broad, the posterior lobes 9–18 cm long (measured along main vein). Leaves uniformly green on both surfaces (midrib and proximal parts of major veins white in *Croat 52023*), matte and dark green above, much paler below and minutely covered with reddish brown scurf; major veins sunken above, the smaller veins conspicuous beneath, darker than the lamina. Inflorescence solitary (or perhaps occasionally paired), peduncle 6–17 cm long. Spathe 8–12 cm long; tube green to purplish, 4–5 cm long; blade white, 5–8 cm long. Spadix ca. 7.5–9.5 cm long; female part of spadix ca. 1.5–2.5 cm long; sterile part 1.5–2.5 cm long; male part 4–4.5 cm long, white. Pollen in monads, inaperturate, subspheroidal, perfectly psilate, 34–43 μm (mean 38 μm) diam., starch-bearing, trinucleate.

Distribution. *Caladium lindenii* var. *sylvestre* is currently known from the departments of Antioquia and Chocó, Colombia, and the Province of Panamá, Panama. It has been collected mostly in deep, shaded primary forest, on slopes near creeks, from near sea level to about 600 m; the label on *Denslow 2672* reads "common in second growth."

The population of *Caladium lindenii* recently discovered along the El Llano–Cartí Rd. in central Panama represents the first known indigenous occurrence of this genus outside the South American continent (see Croat, 1979; Madison, 1981).

The seven flowering collections were made in February, March, April, August, and October.

The vulgar name "picha de gato" is recorded on the label of *Folsom et al. 5785.*

Caladium lindenii var. *sylvestre* differs from the "typical" var. *lindenii* in its plain green, unvariegated leaves. According to the description of *C. lindenii* provided by Madison (1981), var. *sylvestre* would also appear to differ in having considerably larger overall dimensions—especially with regard to leaf measurements, petiole length, peduncle length, spathe length, and the length of the male portion of the spadix. In all of these categories, the ranges of measurements for the two varieties overlap scarcely if at all. That the two forms are nonetheless conspecific is indicated by their distinctive sagittate leaf shape and tangled, reddish brown, scurfy indumentum, as well as by the tendency toward whitening of the major veins seen in one collection of var. *sylvestre.* In any case, the purported size difference is spurious, since many specimens of var. *lindenii* (e.g., *Hutchison 8456,* MO) are every bit as large in all respects as var. *sylvestre.* Madison's measurements must have been taken from a poorly grown specimen, or a particularly small cultivar.

The rediscovery of *Caladium lindenii* in the wild as a plain green-leaved form suggests the possibility that other rare aroid species currently known only from variegated specimens (e.g., *Zomicarpella maculata* N. E. Br.) may also prove to have predominantly concolorous foliage in the wild state. Horticulturists have long favored oddities such as variegated foliage, and it is not unreasonable to suggest that collectors in search of ornamental subjects might have bypassed whole populations of plain green-leaved individuals, pausing only to dig up the occasional attractive, yet anomalous specimen—which, when shipped back to Europe, may well have come to "typify" certain species. This is clearly what must have happened in the case of *Caladium lindenii* and is also suspected in other aroid species such as the familiar "pothos" of horticulture, which is unknown in the wild state. Known variously as *Scindapsus aureus* Engl., *Rhaphidophora aurea* (Engl.) Birdsey and, most recently, *Epipremnum aureum* (Engl.) Bunting, it is now believed to represent nothing more than a variegated form of the widespread Asian species *E. pinnatum* (L.) Engl. (Nicolson, 1978).

Specimens examined. COLOMBIA. ANTIOQUIA: municipio of Anorí, *Soejarto et al. 3197* (MO); Río Anorí valley, *Shepherd 533, 647* (WIS), *Denslow 2672* (WIS); between San Luis and Puerto Triunfo, *Croat 52023* (MO). CHOCÓ: between Quibdó and Istmina, *Croat & Cagallo 52150* (MO); near Río Iró, S of Istmina, *Croat 57398* (MO); region of Río Baudó, *Fuchs 22269* (COL); Serranía de Baudó, between Las Animas and Pato, *Croat 56094* (MO).

PANAMA. PANAMÁ: El Llano–Cartí Rd., *Folsom et al. 5785* (MO), *Hammel et al. 11341* (MO), *Hammel & Kress 13392* (DUKE).

CHLOROSPATHA

The genus *Chlorospatha,* regarded for nearly a century as monotypic, owes its present status as a moderately sizable genus to Madison's (1981) realization that *C. kolbii* Engl., the original species, differed from several species then constituting the genus *Caladiopsis* only in its possession of compound leaves. This being a character of no significance at the generic level among New World Colocasioideae, the two genera were combined under the older name.

As indicated previously, the genus *Chlorospatha* has never before been reported from outside the South American continent. Plants belonging to this taxon have, in fact, frequently been collected from Panama over the past decade; the specimens, however, have generally been misfiled with the more familiar genus *Xanthosoma.* The two genera may be easily distinguished on the basis of vegetative (*Xanthosoma* is frequently cormose; *Chlorospatha* never is) and floral characters (*Chlorospatha* has more slender and elongate inflorescences on more delicate peduncles, with the female portion of the spadix usually at least partly adnate to the spathe). For further details, the reader is referred to the important paper of Madison (1981).

Chlorospatha and *Xanthosoma* are also palynologically distinct; indeed, the first indication that the two mainly Panamanian species described below were members of the genus *Chlorospatha* was provided by an examination of fresh pollen, without recourse to sporophytic material. The two genera are unique in Araceae in shedding pollen in permanent tetrads; as Madison (1981) has indicated, the individual grains (as well as the tetrads) of *Chlorospatha* average considerably smaller than those of *Xanthosoma*—more than 50% smaller, in fact (Grayum, 1984). In addition, pollen of *Chlorospatha* lacks starch and is basically binucleate, whereas pollen of *Xanthosoma* is always starchy and frequently trinucleate (see Grayum, 1985, 1986). In all of these respects, the two species described here are typical members of the genus *Chlorospatha.*

Chlorospatha croatiana Grayum, sp. nov. TYPE: Panama. Coclé: N slope and summit of Cerro Pilón, 900–1,173 m, *Croat 22932* (holotype, MO; isotypes B, K, PMA, US).

Planta terrestris; caulis erectus, subterraneus, saltem ad 22 cm longus; folia singulares paucive, lamina adulta 5–9-pedatisecta, glabra; petiolus (35–)50–70(–83) cm longus, purpureo-maculatus; lamina segmentum medium subaequilaterale, (17–)21–31(–43) cm longum, (6–)9–15(–20) cm latum, anguste ad late ellipticum; segmenta lateralia inaequilateralia. Inflorescentia ad usque 5–6; pedunculus 13–33(–48) cm longus, purpureus; spatha sub anthesi angusta, 7–9 cm longa; tubus (3–)4–6 cm longus, ad 7–9 cm longus in statu fructiferae, intus purpureus; spathae lamina alba, aliquanto cucullata; spadix 3.9–6.1 cm longa; pars feminea 1.2–2.4 cm longa, in dimidio inferiore spatha adnatae; pars sterilis 0.5–1.2 cm longa; pars mascula 2–2.7 cm longa; fructus albus; semina 15–25, alba, striata, ovoidea, 1–1.5 mm longa.

Terrestrial herb 0.5–2 m tall, the sap milky (e.g., *Churchill 3804*). Stems basally decumbent to erect, 5–22 cm or "sometimes ca. 1 m" (*Croat 22932*) long, 0.6–2.5 cm wide (dried), largely subterranean, clothed with weathered brownish and whitish cataphyll fibers. Leaves solitary or few, the petioles (35–)50–70(–83) cm long, terete, green and mottled with purple, at least toward the base, or else solid purple or purple-brown, vaginate in the lower one-fourth to one-half; lamina of adult leaf pedately 5–9-foliolate, glabrous, the central lobe more or less symmetrical, (17–)21–31(–43) cm long, narrowly to broadly elliptical, (6–)9–15(–20) cm broad, usually with 6–7 primary lateral veins per side. Lateral lobes progressively smaller than the central lobe, asymmetrical, the laminar tissue decurrent onto the upper side of the costae at base. Outermost lobes (second pair) acute to truncate, cordate or hastate at the base on the posterior side, only rarely (*Croat 49172*) differentiated basally into an additional (third) pair of lobes. Cataphylls lanceolate, 9–13(–20) cm long, drying reddish brown, persistent and becoming fibrous. Inflorescences up to 5–6, the peduncles 13–33(–48) cm long, purple. Spathe 7–9 cm long at anthesis, narrow, (4.5–)6–9 mm broad, slightly constricted centrally; spathe tube (3–)4–6 cm long at anthesis, green, purplish within, to 7–9 cm long in fruit; blade white to cream, curved forward and somewhat hooded, abscising soon after anthesis. Spadix 3.9–6.1 cm long, stipitate basally for 2.5–6

(–10) mm, the female portion 1.2–2.4 cm long, adnate to the spathe in the basal half (or apparently not at all in *Folsom 5870*); pistils more or less conical; sterile region 0.5–1.2 cm long, pink (*Dressler 4884*); staminodia all connate, the synandrodia drying pale with orange chromoplasts, subprismatic, flat-topped; male portion of the spadix 2–2.7 cm long, broadest at the base or toward the middle. Spadix (male portion?) variously reported as white or cream (*Hammel 3528, Dressler 4884, Knapp & Dressler 3471*) or purple (*Hammel 2571*). Fruits (in *Madison 775, Sytsma et al. 4244, Churchill 3804*) white, ca. 3–5 mm diam., 15–25-seeded. Seeds ovoid, white, longitudinally striate, 1–1.5 mm long, minutely brown-strophiolate. Pollen (pictured in Grayum, 1984) in planar tetrads, inaperturate, coarsely foveolate or reticulate, the individual grains 24–31 μm (mean 27 μm) diam., starchless, binucleate.

Distribution. *Chlorospatha croatiana* ranges from the Atlantic slope of central Costa Rica, southward throughout Panama and into northwestern Colombia.

The new species is named for Thomas B. Croat of the Missouri Botanical Garden, the foremost authority on Central American Araceae, one of whose ample collections has been selected as the holotype.

Chlorospatha croatiana can be divided at the outset into two subtaxa. Since these appear to be allopatric, they are here accorded the rank of subspecies.

Chlorospatha croatiana Grayum ssp. **croatiana.**
Figures 1, 2.

The "typical" subspecies is distinguished by its consistently 5-foliolate (very rarely 7-foliolate) leaves and Central American distribution.

Distribution. The first collection of ssp. *croatiana* was made in Limón Province, on the Atlantic slope of Costa Rica, in 1924 (*Standley 37356*). This remains the only known collection of the species from Costa Rica, and also represents the most northerly station for the genus as a whole. This sterile collection might be mistaken for *Xanthosoma pentaphyllum* (Vell.) Engl. (= *X. hoffmannii* Schott; see Bunting, 1979), which occurs on the Pacific slope of Costa Rica; the locality is suspicious, however, and the inclusion of the apical 2–3 cm of the clearly non-cormose caudex bearing the whitish and reddish brown cataphyll fibers characteristic of *C. croatiana* leaves little doubt as to the identity of the specimen.

This subspecies is most widely distributed in Panama. It is now known from every province except Herrera, Los Santos, and Veraguas—and will certainly turn up in the latter eventually. *C. croatiana* ssp. *croatiana* has been collected on wet slopes and along creeks, mostly in cloud forest, on either side of the continental divide, from 300 to 1,400 m (but mostly from 700 to 1,000 m). The Darién and Puerto Obaldía (San Blas) stations are so near the Colombian border that the subspecies will undoubtedly be found there sooner or later.

Flowering collections of ssp. *croatiana* have been made in all months except November, January, May, and September. The three known fruiting collections were made on 2 May and 22 and 26 October.

Chlorospatha croatiana ssp. *croatiana* is distinct from all other members of the genus except *C. gentryi* (described later in this paper) in its quinquefoliolate leaves. Only three other species of *Chlorospatha*—*C. kolbii, C. mirabilis* (M. T. Mast.) Madison and, the recently described, *C. corrugata* Bogner & Madison (Bogner, 1985)—are known to possess compound or essentially compound leaves. Both *C. kolbii* and *C. mirabilis* were briefly in cultivation during the late nineteenth and early twentieth centuries, and are believed to have originated from northern South America (see Madison, 1981). For the better part of the past hundred years, however, these species have been known collectively from just three herbarium specimens and a few illustrations (Madison, 1981). Though the possibility was considered that the Panamanian entity might represent one of these forgotten species, it does not agree well with the description of either (see Engler & Krause, 1920; Madison, 1981).

Chlorospatha kolbii differs from ssp. *croatiana* in its more numerous (seven to nine) and much shorter and narrower leaflets, supposedly scabrous above and with crispate-undulate margins, shorter and more slender petioles, shorter peduncles, and more prominently stipitate spadix with the female portion fully adnate to the spathe and the lower sterile flowers distinct.

Chlorospatha croatiana ssp. *croatiana* is more similar in overall dimensions to *C. mirabilis*. Two previously unidentified and uncited collections of the latter species were discovered and studied

during the course of the present investigation: *Killip 35091* (COL) and *Croat 56133* (COL), both from the Chocó region of Colombia. Living material of the latter collection is presently in cultivation at the Missouri Botanical Garden. Yet another recent Colombian collection is represented by living material at the Munich Botanical Garden and has been pictured by Bogner (1985). *Chlorospatha mirabilis* differs strikingly from *C. croatiana* in its trifoliolate, usually cream-spotted leaves and larger leaflets, frequently broadly confluent at the base.

The Colombian *Chlorospatha corrugata* is equally distinctive in its trifoliolate, deeply rugose laminae (see Bogner, 1985).

The available material of *C. croatiana* ssp. *croatiana* is somewhat variable, especially with respect to leaflet size and shape; but although occasional specimens appear distinctive in certain aspects (most notably *Hammel & Kress 13401*, from 300 m), a considerable range of this sort of variation is evident even within single populations (see especially *Luteyn & Kennedy 1804*). Thus I have little doubt that the collections listed hereunder all pertain to a single taxon.

Vegetatively, *C. croatiana* ssp. *croatiana* might be confused with some species of *Xanthosoma* with pedately compound leaves. The only one of these occurring in Panama is the widespread *X. helleborifolium* (Jacq.) Schott, which, unlike ssp. *croatiana*, is cormose and generally has narrower and more numerous (11–17) leaflets. Many species of *Syngonium* have pedately compound leaves, however all are scandent.

Specimens examined. COSTA RICA. LIMÓN: vicinity of Guápiles, *Standley 37356* (US).

PANAMA. BOCAS DEL TORO: Fortuna–Chiriquí Grande rd., 4.3 mi. N of Continental Divide, *Croat & Grayum 60208* (MO); 1.1 mi. W of Fortuna–Chiriquí Grande rd. near Continental Divide, *Croat & Grayum 60343* (MO). CHIRIQUÍ: Fortuna–Chiriquí Grande rd., 4.5–5 mi. N of dam, *Croat & Grayum 60078* (MO). COCLÉ: vicinity of Alto Calvario and near sawmill above El Copé, *Maas et al. 2740* (U), *Folsom 5870* (MO), *Hammel 2571, 3528* (MO), *Hammel & Kress 11329* (DUKE), *Croat 49172* (MO), *Knapp & Dressler 3471* (MO); N of El Valle de Antón, *Luteyn 3155* (DUKE); Cerro Pilón, *Croat 22932* (MO). COLÓN: headwaters of upper Río Piedras, *Sytsma et al. 4244* (MO). DARIÉN: Cerro Pirre, *Folsom 4340* (MO). PANAMÁ: Cerro Campana, *Bartlett & Lasser 16938* (MICH, MO), *Luteyn & Kennedy 1804* (DUKE), *Madison 775* (HUH), *Croat 22815* (MO); Río Pequení, 10–15 min. upstream from hydrographic station by motor, *Dressler 4884* (MO); between Tortí and Pilota del Toro, *Folsom et al. 5058* (MO); El Llano–Cartí Rd., *Hammel & Kress 13401* (DUKE); *Churchill 3804* (MO). SAN BLAS: forest SE of Puerto Obaldía, *Croat 16818* (SCZ); headwaters of Río Cangandi, *Hammel & de Nevers 13593* (MO).

Chlorospatha croatiana ssp. **enneaphylla** Grayum, ssp. nov. TYPE: Colombia. Boyacá: El Humbo, 130 mi. N of Bogotá, *Lawrance 794* (holotype, K).

A *Chlorospatha croatiana* ssp. *croatiana* lamina 7–9-pedatisecta differt.

A few Colombian collections exist of an entity that appears to be conspecific with *Chlorospatha croatiana*. Though agreeing with the Central American collections of ssp. *croatiana* in floral morphology and most vegetative characters, it differs consistently in having more leaflets. All three Colombian specimens with mature leaves are 7–9-foliolate, whereas only a single Central American specimen of the 23 examined exhibited even as many as seven leaflets. It seems appropriate, then, that the Colombian entity should receive taxonomic recognition.

Distribution. *Chlorospatha croatiana* ssp. *enneaphylla* is known only from northwestern Colombia, from the departments of Antioquia and Chocó and the western panhandle of Boyacá. Recorded elevations range from 350 to 600 m. The only dated flowering collection (*Shepherd 899*) is from 5 August.

This taxon may be distinguished from vegetatively similar species of *Xanthosoma* inhabiting the region by its caulescent, rather than cormose, habit and its slender and delicate peduncles and inflorescences.

The two collections from Chocó are of sterile and presumably juvenile material; they are placed here speculatively, since they are atypical in leaf size and morphology.

Specimens examined. COLOMBIA. ANTIOQUIA: Río Anorí valley, *Shepherd 899* (WIS). BOYACÁ: El Humbo, *Lawrance 794* (K). CHOCÓ: between Medellín and Quibdó, *Croat 49311, 55930* (MO).

Chlorospatha hammeliana Grayum & Croat, sp. nov. TYPE: Panama. Coclé: just N of sawmill above El Copé, ca. 1,000 m, *Hammel & Kress 13465* (holotype, MO). Figures 3–6.

Planta terrestris; caulis saltem ad 8 cm longus; petiolus 40–65 cm longus, aliquanto spongiosus; lamina glabra, membranacea, simplex, ovata, basi profunde cordata vel sagittata; lobus anticus 23–35 cm longus, 16–27 cm latus; lobus posticus (9–)14–18 cm longus. Inflorescentiae 2–3; pedunculus 25–40 cm longus; spa-

FIGURES 1–4.—1, 2. *Chlorospatha croatiana* Grayum, sp. nov., ssp. *croatiana, Croat 22815.*—3, 4. *Chlorospatha hammeliana* Grayum & Croat, sp. nov., *Croat 44589* (this is a greenhouse-grown specimen; the leaves are disproportionately small as compared with wild-collected material). Photos by Thomas B. Croat.

tha angusta, 9–12 cm longa; tubus intus purpureus; spathae lamina alba vel subviridis; spadix 5.4–7.5 cm longa, pars feminea spathae adnatae ¼ to ⅓ longitudinis, 2.4–3.5 cm longa; pars sterili 1.4–2.2 cm longa; pars mascula alba, aliquanto clavata, 1.6–2 cm longa.

Terrestrial herb; stem appearing erect, 1–1.5 cm thick when dried, to at least 8 cm tall. Petioles 40–65 cm long, terete, somewhat spongy (i.e., easily compressible), glabrous, vaginate only in the basal one-sixth to one-fourth. Lamina of flowering individuals glabrous, simple, ovate, prominently cordate to sagittate basally, the anterior lobe 23–35 cm long, 16–27 cm broad, the posterior lobes (9–)14–18 cm long (measured along main vein). Lamina drying membranaceous and strongly bicolored (much paler below, with dark primary and secondary veins). Posterior costae denudate for 0.5–1.5 cm. Inflorescences 2–3, the peduncle 25–40 cm long. Spathe 9–12 cm long, narrow, constricted at summit of tube. Spathe tube greenish externally, purplish within; spathe blade white or greenish white, abscising after anthesis. Spadix 5.4–7.5 cm long; female portion 2.4–3.5 cm long, adnate to spadix

only in the basal one-fourth to one-third; female flowers pale, more or less conical, 2–2.2 mm long, with spreading, discoid style about the same diam. as the base of the ovary; stigmas yellowish; sterile part of spadix 1.4–2.2 cm long; synandrodia columnar or irregularly prismatic, 0.7–2.2 mm diam., more widely spaced than the fertile male flowers, whitish with reddish chromoplasts, the basal ones sometimes 4–6-lobed or divided. Fertile male region ca. 1.6–2 cm long, white, somewhat clavate; synandria prismatic, 4–5-thecate, truncate at apex, closely spaced. Pollen in planar tetrads, inaperturate, minutely rugulate or verruculate, the individual grains 23–25 μm (mean 24 μm) diam., starchless, binucleate.

Distribution. *Chlorospatha hammeliana* is known only from two isolated areas astride the Continental Divide in west-central Panama. At the type locality, near El Copé in Coclé Province, it occurs on steep slopes in very wet cloud forest on the Atlantic slope at 900–1,000 m. Two other sterile collections are from the area of Cerro Tute, near Santa Fe, Veraguas Province, at 700 m on the Atlantic slope and 1,050–1,150 m on the Pacific.

The single wild flowering collection (the holotype) was made on 25 August. (*Croat 44589* also includes fertile material, however the original wild collection was sterile; a live voucher flowered later in the greenhouse at the Missouri Botanical Garden—see Figs. 3–6—and was added to the collection.)

Chlorospatha hammeliana must be considerably rarer than *C. croatiana,* or perhaps it occurs in a more inaccessible habitat. Both species grow in the vicinity of the sawmill above El Copé, a popular collecting locality; but although *C. croatiana* seems to have been collected by virtually every botanist who has visited the site, *C. hammeliana* has been found but twice.

The new species is dedicated to Barry E. Hammel, now of the Missouri Botanical Garden, ardent and perspicacious collector and monographer of the flora of southern Central America, who first brought this plant to our attention.

Chlorospatha hammeliana is perhaps most similar to the Ecuadorian *C. besseae* Madison (1981; validated in Selbyana 7: 353. 1984, and again by Bogner, 1985), which likewise has simple, cordate leaves. That species, however, has shorter petioles and peduncles, smaller laminae, a smaller inflorescence, and orange male flowers. Furthermore, the female portion of the spadix in *C. besseae* is said to be completely adnate to the spathe.

Specimens examined. PANAMA. COCLÉ: N of sawmill above El Copé, *Croat 44589* (MO), *Hammel & Kress 13465* (MO). VERAGUAS: along trail to top of Cerro Tute, *Croat 48895* (MO); along Santa Fe–Calovébora rd., *Croat 48993* (MO).

During the course of the present investigation, yet another undescribed species of *Chlorospatha* was discovered among the collections of the Missouri Botanical Garden. This particularly distinctive species, from the Cordillera Occidental of northern Colombia, is described below. Though the male portion of the spadix (hence, the pollen) is unknown, the specimens conform in all other important respects to the most recent circumscription of *Chlorospatha* (Madison, 1981), to which the new species is therefore assigned without hesitation.

Chlorospatha gentryi Grayum, sp. nov. TYPE: Colombia. Antioquia: trail from Encarnación to Parque Nacional de los Orchídeas, W slope of Cordillera Occidental, 1,600–1,800 m, *Gentry & Rentería A. 24585* (holotype, MO-2715461; isotypes, COL, HUA). Figure 7.

Planta terrestris; caulis erectus saltem ad 10 cm longus; petiolus 12–20 cm longus, furfuraceus versus apicem; lamina 5-pedatisecta, secus venas venulasque subtus crispato-puberula, margine crispato-undulata; costa furfuracea; segmentum medium laminae aequilateralis, ellipticum, 6.5–9.5 cm longum, 3–4 cm latum; segmenta lateralia valde inaequilateralia. Inflorescentiae 2–3; pedunculus 6.5–9 cm longus, furfuraceus praesertim versus apicem; tubus spathae 2–2.5 cm longus, non nisi dorso extrinsecus dense furfuraceus, viridis, tenuibis longitudinalibus multinervis; spathae lamina alba; spadix pars feminea ca. 1.9 cm longa, sessilis, in dimidio inferiore spathae adnatae; spadix pars mascula ignota.

Terrestrial herb; stem erect, to at least 10 cm tall, 6–9 mm thick when dried. Petioles 12–20 cm long, slender, vaginate in basal one-fourth to one-third, clasping the stem, scurfy-pubescent with more or less flattened, branched, multicellular hairs in the apical one-half to one-fourth. Lamina pedately 5-foliolate, the margins crispate-undulate; lamina glabrous above, paler below and crispy-puberulent along the veins of all orders; costae naked or obscurely alate, with an indumentum like that of the upper petioles. Central lobe of lamina symmetrical or nearly so, elliptical, 6.5–9.5 cm long, 2.5–4 cm broad; lateral

FIGURES 5–7.—5, 6. *Chlorospatha hammeliana* Grayum & Croat, sp. nov., *Croat 44589*. Photos by Thomas B. Croat.—7. *Chlorospatha gentryi* Grayum, sp. nov., *Gentry & Rentería 24585* (Type). Photo by Alwyn H. Gentry.

lobes strongly asymmetrical, progressively smaller; all lobes acute at the base. Inflorescences 2–3, the peduncles 6.5–9 cm long, more or less densely crispy-puberulent especially in the apical part, the indumentum extending in a dense patch onto the dorsal surface of the spathe tube; spathe tube 2–2.5 cm long at anthesis, ca. 5 mm diam., greenish, finely longitudinally many-nerved; blade whitish, abscising soon after anthesis. Female part of spadix ca. 1.9 cm long, sessile (i.e., not stipitate), adnate to the spathe in the basal half. Male part of spadix unknown.

Distribution. To date, *Chlorospatha gentryi* is known only from the holotype, collected at 1,600–1,800 m on the western slope of the Cordillera Occidental in Antioquia Department, Colombia.

Chlorospatha gentryi, in its small, pedately-compound leaves with crispate-undulate margins, immediately recalls the elusive *C. kolbii.* It differs from that species, however, not only in its 5- rather than 7–9-pedatisect leaves, but also in its even shorter petioles and peduncles, non-stipitate spadix and crispy-puberulent indumentum (Engler & Krause, 1920, described the lamina of *C. kolbii* as "subholosericea," but only on the upper surface).

The new species is named for the collector of the holotype specimen, Alwyn H. Gentry of the Missouri Botanical Garden, one of the most active and authoritative field botanists working in the neotropics and a specialist on the flora of Pacific South America.

Specimens examined. COLOMBIA. ANTIOQUIA: trail from Encarnación to Parque Nacional de las Orchídeas, W slope of Cordillera Occidental, *Gentry & Rentería A. 24585* (MO, COL, HUA).

Inasmuch as the present paper significantly augments the number of compound-leaved *Chlorospatha* species known, a key to this assemblage is provided below:

KEY TO THE SPECIES OF *CHLOROSPATHA* WITH COMPOUND LEAVES

1a. Lamina trifoliolate, the leaflets narrowly to broadly confluent basally 2
2a. Lamina deeply rugose, concolorous; lateral lobes nearly equaling median lobe; petiole less than 50 cm long ..... *C. corrugata* Bogner & Madison
2b. Lamina relatively plane, frequently spotted with pale yellow or cream; median lobe nearly twice as long as lateral lobes; petiole more than 50 cm long ..... *C. mirabilis* (M. T. Mast.) Madison

1b. Lamina 5–9-foliolate, the leaflets narrowly confluent at the base or not at all 3
3a. Lamina large, the central lobe more than 15 cm long and 5 cm broad; leaf margins plane; petioles more than 33 cm long 4
4a. Lamina 5-(rarely 7-)pedatisect; southern Central America ..... *Chlorospatha croatiana* Grayum ssp. *croatiana*
4b. Lamina 7–9-pedatisect; Colombia ..... *Chlorospatha croatiana* ssp. *enneaphylla* Grayum
3b. Lamina small, the central lobe less than 15 cm long and 5 cm broad; leaf margins crispate-undulate; petioles less than 33 cm long 5
5a. Lamina 5-pedatisect; petioles less than 25 cm long; peduncles less than 12 cm long; veins on lower side of leaf, costae, apical portions of petiole, peduncles and dorsal surface of spathe tube crispy-puberulent; spadix sessile ..... *Chlorospatha gentryi* Grayum
5b. Lamina 7–9-pedatisect; petioles more than 25 cm long; peduncles more than 12 cm long; foliage not crispy-puberulent; spadix stipitate by 1.5 cm ..... *Chlorospatha kolbii* Engl.

With the addition of *Chlorospatha corrugata* Bogner & Madison and the three species just described to Madison's (1981) previous total of 11, the number of species now attributable to this suddenly burgeoning genus stands at 15. This represents nearly a fourfold increase in less than a decade (cf. Madison, 1978), occasioned by the installation of a clearly articulated generic circumscription coincident with the exploration of rich new habitats. Judging from the present rate of discovery and the number of intriguing sterile specimens filed away in herbaria, it seems likely that *Chlorospatha,* which lay dormant for nearly a hundred years, will eventually come to comprise as many as 20–25 species. The Chocó region of Colombia, which appears to be a stronghold of the genus, is one of the most botanically diverse and least-known areas remaining on the planet (Gentry, 1982), and can be expected to yield many interesting new species of Araceae. Perhaps it will also eventually yield additional material of the type species of *Chlorospatha, C. kolbii,* which, somewhat perplexingly, continues to elude rediscovery.

XANTHOSOMA

Over the past ten years, generic concepts in the tribe Caladieae have been arduously tested, mainly due to a major influx of specimens, comprising many new species, from the Andean re-

gions of Colombia, Ecuador, and Peru. *Chlorospatha*, not even recognized in its present circumscription a decade ago, has ironically emerged as perhaps the most distinctive of the three polytypic genera. It is well characterized by its caulescent habit, slender inflorescences with the female portion of the spadix usually fused with the spathe, widely spaced female flowers with thin, deliquescent, mantle-like styles dotted with red chromoplasts, oddly shaped synandrodia and small, starchless pollen borne in tetrads (Madison, 1981; Grayum, 1985).

The definitions of *Caladium* and *Xanthosoma* have, on the other hand, become more nebulous over the past ten years. In 1976, Michael Madison, who has made a specialty of this group and significantly clarified its taxonomy, published a list of six mainly vegetative and habital criteria that, he believed, could be used to distinguish *Caladium* from *Xanthosoma*. In all of these attributes—plant size (less than 0.5 m tall), habitat (not weedy), stem morphology (a globose tuber), peduncle length (relatively long), inflorescence number (solitary), and petiole attachment (peltate)—the species described below would fall more or less clearly into *Caladium*. In actual fact, however, several species of *Xanthosoma* were already known that violated one or more of these rules, and, in subsequent years, numerous additional aberrant species were described. The distinctions between the two genera finally became so blurred that, by 1981, Madison was forced to admit that "the single inflexible character separating them is the shedding of pollen in tetrads in *Xanthosoma* and in solitary grains in *Caladium*."

With the discovery of the following species, unique in violating all six of the above guidelines, the beleaguered generic concepts of *Xanthosoma* and *Caladium* have been subjected to their most formidable challenge yet—from which they emerge, I believe, unscathed, vindicated, and even reinforced.

Xanthosoma caladioides Grayum, sp. nov. TYPE: Panama. Comarca de San Blas, coast NE of Puerto Obaldía towards Colombian border, 8°40′N, 77°25′W, sea level, *Knapp & Mallet 4687* (holotype, MO-2982678). Figures 8, 9.

Planta terrestris vel epilithica, cormifera; petiolus 17–58 cm longus, ut videtur glaucus, laminae peltatim affixus; lamina glabra, membranacea, subtus glauca, simplex, ovata, basi cordata; lobus anticus 11–25 cm longus, 9–25 cm latus; lobus posticus 3.9–12.5 cm longus, rotundatus; distantia insertione petioli sinui laminae 2.7–5.5 cm. Inflorescentia solitaria; pedunculus (10.5–)12.5–33 cm longus; spatha sub anthesi 6.5–11 cm longa; tubus 2.5–5 cm longus, extus viridis, intus purpureus; spathae lamina (3.3–)4.3–6.3 cm longa, alba; spadix 5.3–9.8 cm longa, sessilis; pars feminea 1.6–2.9 cm longa, spathae vix adnatae; styli lati, discoidei, patuli; spadix pars sterili 1.4–2.7 cm longa, inferne dilatata, superne angustata; pars mascula 2.7–4.6 cm longa, 5–7 mm diametro, alba. Semina ca. 40–50, brunnea, tenuiter multicarinata, ovoidea, 0.8–1 mm longa. Pollinis granula quaternatim aggregatae.

Terrestrial or epipetric, acaulescent, cormose herb, ca. 25–50 cm tall. Corm subglobose, 1.5–2.5 cm diam. when dried. Leaves and "stems" (presumably petioles) glaucous (*Knapp & Mallet 4687*); petioles 17–58 cm long, vaginate in basal one-eighth to one-third, peltately attached. Lamina of adult leaf glabrous, drying membranaceous, glaucous below, apparently plain green above (*Allen 4629* appears to have darker markings, but the label is uninformative), simple and ovate, cordately lobed at the base, asymmetrically acute apically, the margins entire; anterior lobe (measured from insertion of petiole) 11–25 cm long, 9–25 cm broad, the posterior lobes (measured along main vein from insertion of petiole) 3.9–12.5 cm long, rounded; distance from petiole insertion to base of sinus 2.7–5.5 cm, the sinus more or less acute. Inflorescences 1 or 2 per plant, solitary in the sheaths, the peduncles (10.5–)12.5–33 cm long. Spathe 6.5–11 cm long at anthesis, constricted centrally; spathe tube 2.5–5 cm long at anthesis, ca. 1.4–2.3 cm broad when pressed, green externally, purple within, to ca. 6 cm long in fruit; blade (3.3–)4.3–6.3 cm long, white, abscising after anthesis. Spadix 5.3–9.8 cm long, slightly shorter than the spathe, sessile, the female portion 1.6–2.9 cm long, adnate to the spathe for 5 mm or less; pistils broadly conical, surmounted by a broad, spreading, discoid style, the ovary apparently with 3 partitions; sterile region of spadix 1.4–3.5 cm long, the basal third thicker than the female region, with the flowers bulbously enlarged, the apical two-thirds stipitate, narrower than the male region, the flowers vertically elongated and flattened; male portion of the spadix 2.7–4.6 cm long, widest in middle, ca. 4–7 mm broad when pressed, white; synandria flat-topped, roughly polygonal, with the margins sinuate, 0.5–2.2 mm in greatest diam., the anthers ca. 1.5 mm long and somewhat curved, dehiscing by apical pores. Fruits (in *Stern et al. 444*) ca. 3–3.3 mm diam. and whitish, when dried; seeds ca. 0.8–1 mm long, ovoid, brown, with 12–14 narrow, longitudinal keels; at least 45 counted in one intact fruit (*Bristan 1074*).

Distribution. *Xanthosoma caladioides* was first collected by Paul Allen in 1947 from Darién Province, Panama. It is still known from only eight collections, all from the Province of Darién and the Comarca of San Blas, in easternmost Panama. The three San Blas collections are all from near or at sea level, from near the Colombian border west to the vicinity of Playón Chico. Two of the Darién collections are from below 100 m in the valley of the Río Tuira, but *Allen 4629* was collected at 500–700 ft. on the inland slope of the Atlantic coastal range, and *Bristan 1074* appears to have come from the same general area. *Hammel 7314,* on the other hand, is from about 500 ft. in the remote Serranía del Sapo, fronting the Pacific coast. Thus, though little collected in this poorly explored end of Panama, *X. caladioides* is clearly widespread there. It certainly ranges into adjacent Colombia as well, at least along the Urabá coast, and perhaps into the Río Atrato basin, but no definite South American collections have been seen. A recent sterile collection (*Hammel 14162,* MO) of an unknown peltate-leaved aroid from primary forest on limestone at about 600 m in southwestern Costa Rica may also belong here.

Xanthosoma caladioides apparently may be either terrestrial or epipetric. The holotype, from San Blas, was collected in "tropical dry forest" with "strong sea winds"; the other two San Blas collections were from "coastal rocks . . . near the sea" (*D'Arcy 13692*) and in sandy soil, in deep shade in secondary growth (*Stier 34*). Two of the Darién collections were from along streambanks ("very common on steep, shaded banks," *Allen 4629*; "on slopes along stream," *Hammel 7314*), whereas *Stern et al. 444* was "growing on a vertical stone wall."

All of the recognizable collections of *Xanthosoma caladioides* are fertile, and all were made between 18 April and 30 June—the later collections representing mostly fruiting material. This period marks the onset of the rainy season in most of Panama (Foster, 1985). It is conceivable that *X. caladioides* passes much of the dry season in a leafless condition, as do several other species of the genus (pers. observ.).

No information is available on pollination of *Xanthosoma caladioides.* I have noted that inflorescences at the anther-dehiscent stage (e.g., *Allen 4629, Stier 34*) tend to be lacking the enlarged basal sterile flowers, suggesting that these may serve as food-rewards for the pollinators (presumably dynastine scarab beetles).

Although one would not have anticipated the existence of any ethnobotanical information for such an obscure species, the label of *Stier 34* records the following: "kuidar [presumably a common name, in some unspecified indigenous language]—root used against fever."

The new species resembles the familiar, cultivated species *Caladium bicolor* (Ait.) Vent. so strikingly—at least on herbarium sheets—that it has been so determined repeatedly by several leading aroid specialists, including Madison himself. Vegetatively, the two species are virtually indistinguishable from dried material—though the posterior laminar lobes of *X. caladioides* are generally somewhat smaller and less divergent, and presumably the leaves are less frequently and/or less extensively variegated, if at all. (Regrettably, no plant of this species has ever been collected or, to my knowledge, even beheld alive by any aroid specialist, and none of the specimens is accompanied by fully adequate notes.) The resemblance also extends to the external aspect of the inflorescence.

Careful study of the inflorescence morphology, however, clearly reveals not only that the new species is not *Caladium bicolor,* but that it belongs unequivocally in the genus *Xanthosoma.* The first indication of this was provided by an examination of pollen under a compound light-microscope: pollen from all four polleniferous collections (*Stier 34, Allen 4629, Stern et al. 444, Hammel 7314*) was observed exclusively in tetrads. Two other technical, floral characters serve to distinguish *Caladium* and *Xanthosoma* in the vast majority of cases, and in both of these, the new species clearly agrees with the latter genus. First, broad, discoid, spreading styles, characteristic of *Xanthosoma* but lacking in *Caladium,* are plainly evident in the holotype specimen. Second, at least 45 seeds were counted in an intact fruit of *X. caladioides* (from *Bristan 1074*)—considerably above the maximum of 20 tolerated for *Caladium.* The multiovulate nature of *Xanthosoma* ovaries, incidentally, is probably closely correlated with the retention of pollen in permanent tetrads (Madison, 1981).

Two additional floral characters, though taxonomically insignificant at the generic level, may be of practical aid in distinguishing specimens of *Caladium bicolor* and *Xanthosoma caladioides*: the synandria of the former species are deeply notched marginally, whereas those of the latter are merely sinuate; and, the sterile region in *Caladium bicolor* is not so sharply differen-

FIGURES 8–10.—8, 9. *Xanthosoma caladioides* Grayum, sp. nov.—8. *Hammel 7314.*—9. *Knapp & Mallet 4687* (Type), inflorescence.—10. *Caladium bicolor* (Ait.) Vent., *Berry 640* (MO), Venezuela, inflorescence.

tiated into a narrowly stipitate apical portion and a bulbous basal portion, though there is a slight tendency in this regard (Figs. 9, 10).

Xanthosoma caladioides is not the first species of *Xanthosoma* known to have peltate leaves. The precedent was set a decade ago with the description of *X. peltatum* Bunting (1975) from Venezuela, about which the author later remarked: "el encuentro de esta especie andina cambia completamente nuestro concepto del género *Xanthosoma*" (Bunting, 1979). With our concept thus altered, the new species is neatly accommodated in *Xanthosoma.* It does not, however, appear closely related to *X. peltatum*—a much larger and coarser, arborescent plant of higher elevations—and one must suppose independent derivations of peltate leaves in these two species. The general aspect and inflorescence structure of *Xanthosoma caladioides* appear to ally it more closely with *X. mexicanum* Liebm. and related species, intractable violators of Madison's six criteria, from which it may be readily distinguished by its glabrous foliage, in addition to its peltate leaves.

Specimens examined. PANAMA. DARIÉN: Río Tuqueza below Québrada Venado, *Bristan 1074* (MO); headwaters of the Río Chico, *Allen 4629* (MO); Río Paya, near junction with Río Tuira (Boca de Paya), *Stern et al. 444* (MO); Río Pucuro, below village of Pucuro, *Duke 13141* (MO); Río San Antonio, upstream from Garachiné, *Hammel 7314* (MO). SAN BLAS: Playón Chico, Molia, *Stier 34* (MO); coastal rocks between Puerto Obaldía and Puerto Armila, *D'Arcy 13692* (MO); coast NE of Puerto Obaldía, *Knapp & Mallet 4687* (MO).

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NOTE ADDED IN PROOF: *Chlorospatha croatiana* ssp. *croatiana* has recently been recollected in Costa Rica: HEREDIA: forest between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, 10°17.5′N, 84°04.5′W, 700–750 m, *Grayum 6657* (MO).

NEW TAXA IN *OENOTHERA* (ONAGRACEAE)[1]

WARREN L. WAGNER[2]

ABSTRACT

A new species, three new sections, and one new subsection of *Oenothera* are described and a new combination in *O. flava* is made here so that the names will be available. **Oenothera coryi** (sect. *Megapterium*), which ranges from north-central Texas to the southern part of the panhandle, is described. The combination *O. flava* subsp. *taraxacoides* (sect. *Lavauxia*) is made for large-flowered, modally outcrossing populations of *O. flava* from three disjunct areas: 1) Mogollon Plateau, Arizona to Catron Co., New Mexico; 2) Sacramento Mountains and Sierra Blanca in southeastern New Mexico; and 3) Sierra Madre Occidental from Chihuahua to Durango, Mexico. As part of a genus-wide re-evaluation of the infrageneric classification, three new sections, **sect. Ravenia, sect. Eremia,** and **sect. Contortae,** are proposed for species formerly included in subg. *Pachylophus,* which is no longer recognized, and **subsect. Australis** is described for the two white-flowered South American species of sect. *Lavauxia.*

A number of concurrent studies of *Oenothera* are in progress, including studies of flavonoids, seed anatomy and morphology, and pollen morphology. Several new names are published here in order to make them available prior to the publication of detailed revisions of the sections in which they occur. With the publication of this paper and an upcoming paper on the systematics of subsect. *Raimannia* and a related new subsection (Dietrich et al., submitted) all taxa in the genus will have been published that have been recognized in a series of detailed systematic studies initiated in the mid-1960s by Peter Raven. Detailed discussion of the new taxa and one combination presented here will be made in the respective sectional revisions.

OENOTHERA SECT. *MEGAPTERIUM*

This section consists of four species. The most distinctive is *Oenothera macrocarpa* Nutt., a polymorphic species of the Great Plains that is subdivided into four subspecies (Wagner, 1983). The other three species were previously included by Munz (1930) in *O. brachycarpa* A. Gray. Detailed study of morphology, cytology, and distribution showed that Munz's *O. brachycarpa* actually consists of three allopatric species: *O. brachycarpa,* a diploid ($n = 7$) from western Texas to southeastern Arizona and northern Mexico; *O. howardii* (A. Nels.) W. L. Wagner, consisting of tetraploid, hexaploid, and octoploid plants ($n = 14, 21, 28$) from eastern Colorado, Utah, and eastern Nevada (Wagner, 1983); and *O. coryi,* described here, a tetraploid occurring from north-central Texas to the southern Texas Panhandle.

Oenothera coryi W. L. Wagner, sp. nov. TYPE: U.S.A. TEXAS: Taylor Co., eroded red clay soil, Camp Barkeley, 1 July 1943, *W. L. Tolstead 7537* (MO-1266818, holotype; BH 2 sheets, GH, MICH, NEB 2 sheets, NY 3 sheets, SMU, TEX, isotypes).

Oenothera brachycarpa var. *typica* sensu Munz (all material except the type), Amer. J. Bot. 17: 368. 1930, non Munz (as to the type).

Folia linearia ad angusto lanceolata margine integro vel in dimidio inferiore remote pinnatilobato; flores vix odori, petalis flavis mox dilute aurantis; capsula abrupte ad rostrum apicale producta, valva quaque ala marginali 4–6 mm lata praedita.

Acaulescent or caulescent and caespitose perennial herbs from a stout woody taproot with a usually branched caudex sometimes producing clusters of rosettes 10–60 cm across. Leaves linear to narrowly lanceolate, 5–16 cm long, (2–)3–5(–7) mm wide, densely strigillose, apex long-attenuate, acute to rounded, margin entire to the lower half remotely pinnately-lobed. Flowers 1–3, rarely more, opening near sunset, weakly scented. Buds with free sepal tips 0.7–1.2 mm long. Floral tube (5.5–)7.5–10(–12.5) cm long. Petals yellow, fading orange, drying lavender to purple, broadly obovate, 3.5–4.3 cm long, 3.7–4.2 cm wide, sometimes with a terminal tooth ca. 2 mm long. Capsule ovoid in outline, 2.5–3 cm long, usually abruptly constricted to an apical

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beak, each valve with a marginal wing 4–6 mm wide. Seeds in 2 distinct rows per locule, often reduced to one row near the apex, or occasionally only one row throughout, obovoid to subcuboid, angled, dark brown, 2.5–4 mm long, the surface corky and coarsely rugose to furrowed especially on the abaxial surface toward the proximal end, the distal end with a thick ridge on the abaxial and lateral sides of the seed; the testa very thick especially at the distal end, this area with a conspicuous internal cavity adjacent to the embryo. Self-incompatible. Mitotic chromosome number, $2n = 42$.

Distribution. Open grassland or disturbed areas such as roadcuts from Baylor, Knox, Throckmorton, Nolan, Taylor and Callahan counties in north-central Texas and Crosby and Garza counties in the Texas Panhandle, 350–920 m. Flowering in April and May.

Oenothera coryi is named in honor of V. L. Cory (1880–1964), who recognized this plant as a new species but never published it. This new species is equivalent to Munz's *Oenothera brachycarpa* var. *typica* (1930). The type of *O. brachycarpa* A. Gray [Pl. Wright. 1: 70. 1852. TYPE: Between present-day Val Verde and El Paso counties, Texas, July to November 1849, *C. Wright s.n.* (GH, lectotype, photo MO, TEX; US, isolectotype; Munz, Amer. J. Bot. 17: 368. 1930).] is not from west-central Texas as Munz thought, but, based on Charles Wright's itinerary for 1849 (McKelvey, 1955), it appears to have been collected in southwestern Texas between Val Verde and El Paso counties. Thus the plants from west-central Texas need a name. Apparently Munz, who did not know Wright's route at the time, placed the type specimen with others from west-central Texas because of its narrow leaves, although he commented (1930, p. 368) that the capsule wings of the type of *O. brachycarpa* were narrower than all other collections that he placed in his var. *typica*. Narrow wings are typical of *O. brachycarpa*. I am describing this entity endemic to west-central Texas as *Oenothera coryi*. Not only is its range completely separate from that of *O. howardii* to the north and west in Colorado, Utah, and Nevada, and that of *O. brachycarpa* to the south, in western Texas to southeastern Arizona and northern Mexico, but it is also morphologically distinct. *Oenothera howardii*, to which *O. coryi* is most closely related, can be distinguished by its consistently oblanceolate, elliptic, or sometimes lanceolate leaves, strongly scented flowers with a sweet odor, free sepal tips 1–3(–4) mm long in bud, plants usually at least sparsely hirsute, brilliant yellow and usually larger petals (3–)4–7.3 cm long that fade deep red and dry deep reddish purple or reddish brown, and its capsules that gradually taper to a sterile beak. *Oenothera brachycarpa* differs from *O. coryi* in its grayish green leaves usually with a terminal lobe, longer floral tube (9–)12–21(–22) cm long, longer free sepal tips 1–7 mm long, broadly rhombic-obovate petals, and presence of hirsute as well as strigillose pubescence.

OENOTHERA SECTS. *RAVENIA, EREMIA, CONTORTAE* AND *PACHYLOPHUS*

In the most recent evaluation of *Oenothera* subg. *Pachylophus* (Raven, 1970) eight species were included, *O. muelleri* Munz, *O. tubifera* Sér., *O. xylocarpa* Cov., *O. primiveris* A. Gray, *O. caespitosa* Nutt., *O. cavernae* Munz, *O. brandegeei* (Munz) Raven, and *O. macrosceles* A. Gray. In that paper these species were tentatively divided into four groups: *O. muelleri* and *O. tubifera* with white flowers and stout, obtusely angled, nontuberculate capsules; *O. xylocarpa* and *O. primiveris* with yellow flowers and stout, acutely angled, nontuberculate capsules; *O. caespitosa, O. cavernae,* and *O. brandegeei* with white flowers and stout, tuberculate capsules; and *O. macrosceles* with yellow flowers and slender, quadrangular, nontuberculate capsules. Raven (1970) suggested that these eight species were related and could be considered as constituting one somewhat heterogeneous subgenus or alternatively the four subgroups could be recognized as distinct sections.

Recent study of crossing relationships, vegetative, capsule, and seed morphology (Stubbe & Raven, 1979; Dietrich et al., 1985) suggests that *O. macrosceles* is best grouped with *O. maysillesii* Munz, *O. stubbei* Dietrich, Raven & W. L. Wagner, and *O. organensis* Munz in sect. *Oenothera* subsect. *Emersonia* (Munz) Dietrich, Raven & W. L. Wagner. The other species placed in subg. *Pachylophus* fall into four crossing groups whose members cannot be successfully hybridized with species of a different group (Wagner, unpubl.; Stubbe, unpubl.; Raven, 1970): 1) *O. muelleri* and *O. tubifera*; 2) *O. primiveris*; 3) *O. xylocarpa*; and 4) *O. caespitosa, O. brandegeei* and *O. cavernae* (Raven, 1970; Stockhouse, 1973; Wagner et al., 1985). Morphology, especially of

capsules and seeds, and a cladistic analysis support the four crossing groups (Wagner et al., 1985; Wagner, unpubl.). Anatomical evidence from a genus-wide study of seeds (Tobe et al., in press) showed that each of the crossing groups has distinctive anatomical features, although *O. xylocarpa* is very similar to *O. maysillesii* and *O. primiveris*. The *O. caespitosa* group and the *O. muelleri* group have conspicuous, unique, derived features. In view of the narrow sectional concept established by Lewis and Lewis (1955) for *Clarkia* and subsequently followed in all systematic studies of the family, these four groups of *Oenothera* should be recognized as sections. Three of the four sections are described here as new, and sect. *Pachylophus* is now delimited to include *O. caespitosa* and four related species (Wagner et al., 1985). Subgenus *Pachylophus* is no longer recognized. With these adjustments *Oenothera* is divided into 14 sections, each of which is composed of very closely related species that share numerous morphological features, anatomical features, and, based on crossing studies, similar genomes and usually similar plastomes. At present no subgenera are recognized, but work in progress (Wagner & Raven, unpubl.) summarizing all available data for the genus suggests that it may be possible to subdivide it into two subgenera.

I. **Oenothera** L. sect. **Ravenia** W. L. Wagner, sect. nov. TYPE: *Oenothera muelleri* Munz.

Oenothera subg. *Pachylophus* sensu Munz, Amer. J. Bot. 18: 728. 1931, pro parte; N. Amer. Fl. II. 5: 98. 1965, pro parte.
Oenothera subg. *Raimannia* sensu Munz, N. Amer. Fl. II. 5: 104. 1965, pro parte.

Plantae perennes hirsutae strigillosaeque vel subglabrae; tubus floralis recurvus; petala alba; capsula oblongo-lanceolata angulis acutis ad rotundatis; semina respectu morphologia saepe irregularia 3–7 mm longa supervicie adaxali costis longitudinalibus praedita.

Fleshy-leaved perennial herbs; stems several, arising from the rosette, decumbent to ascending. Pubescence of two types: hirsute, the hairs usually with a purple pustulate base and strigillose, the leaves sometimes glabrous. Buds curved downward by the recurved floral tube. Petals white. Capsules oblong-lanceoloid, somewhat curved, the angles acute to rounded, sessile. Seeds in 1 or 2 rows per locule, basically obovoid to oblong or oblanceoloid, often somewhat irregular, 3–7 mm long, the abaxial surface with longitudinal ribs; the testa very thick above the raphe and at the distal end, the thickened area with a cavity not visible externally or rarely appearing as a distal pore and/or a raphial groove. Self-incompatible (*O. muelleri*) or self-compatible (*O. tubifera*), outcrossing or modally autogamous, respectively. Basic chromosome number, $x = 7$.

The two species of this section, *Oenothera muelleri* and *O. tubifera,* have disjunct and presumably relictual ranges in Mexico from 2,300 to 2,500 m in Madrean woodland vegetation. *Oenothera muelleri* occurs in Nuevo Leon, Tamaulipas, and Coahuila, and *O. tubifera* occurs further south and west in the states of Hidalgo, Puebla, Guerrero, and Durango. This section appears to represent a lineage that diverged early in the evolution of the genus from ancestors similar to sect. *Oenothera* subsect. *Emersonia* (Raven, 1970; Stubbe & Raven, 1979; Wagner et al., 1985) and it is the sister group to sects. *Eremia, Contortae,* and *Pachylophus* (Raven, 1970; Wagner et al., 1985). The sectional name is intended to honor Peter H. Raven, who initiated this series of revisionary works on *Oenothera* over 25 years ago and who first placed the species of sect. *Ravenia* together as close relatives in 1970.

II. **Oenothera** L. sect. **Eremia** W. L. Wagner, sect. nov. TYPE: *Oenothera primiveris* A. Gray.

Oenothera subg. *Pachylophus* sensu Munz, Amer. J. Bot. 18: 728. 1931, pro parte; N. Amer. Fl. II. 5: 98. 1965, pro parte.

Plantae annuae hirsutae strigillosae et glanduloso-puberulae; tubus floralis recurvus; petala flava; capsula fere lanceolata ad ovoidea angulis acutis; semina obovoidea ad oblanceolata, 3–3.5 mm longa crasse rugosa, superficie adaxali sulco conspicuo area crassa cum forma U circumcincto.

Winter annual herbs, acaulescent or caulescent; stems when present usually simple, but occasionally with secondary branches arising from near the base, densely leafy, primary stem erect, secondary branches ascending. Pubescence of three types: hirsute, on the stems and ovary, the hairs usually with a reddish purple pustulate base; strigillose; and glandular puberulent. Buds curved downward by the recurved floral tube. Petals deep yellow. Capsule lanceoloid to ovoid, falcate or curved to nearly straight, the angle acute, sessile. Seeds in 2 rows per locule, obovoid to oblanceoloid, 3–3.5 mm long, coarsely rugose on the distal half of the abaxial side, the raphial face

with a conspicuous groove surrounded by a U-shaped, thickened area terminating at a pore near the distal end, the entire surface papillose, the papillae apically depressed; the testa very thick above the raphe and at the distal end, the thickened area with a cavity that appears as a pore near the distal end and a groove along the raphial face. Self-compatible, rarely self-incompatible, outcrossing to autogamous. Basic chromosome number, $x = 7$.

Oenothera primiveris, the only species of this section, is scattered or occasionally locally common in the Mojave, Sonoran, and Chihuahuan deserts, 30–1,600 m, in sandy soils in low desert to mountain foothills. Based on a cladistic analysis, especially utilizing seed morphology, sect. *Eremia* appears to be most closely related to sect. *Pachylophus* (Wagner et al., 1985), a relationship supported by the recent analysis of seed coat anatomy (Tobe et al., in press). The sectional name is the Greek word *eremia,* meaning desert, in reference to the restriction of this section to the North American deserts.

III. **Oenothera** L. sect. **Contortae** W. L. Wagner, sect. nov. TYPE: *Oenothera xylocarpa* Cov.

Oenothera subg. *Pachylophus* sensu Munz, Amer. J. Bot. 18: 728. 1931, pro parte; N. Amer. Fl. II. 5: 98. 1965, pro parte.

Plantae perennes brevi-hirsutae interdum sparse hirsutae; tubus floralis erectus; petala flava; capsula fere lanceolata angulis acutis tortuosis contortis pagina conspicue rugosa; semina grosse rugosa superficie adaxali cristis duabus parvis longitudinalibus praedita.

Acaulescent perennial herbs. Pubescence of two types: short-hirsute, the hairs erect to curved and somewhat appressed; occasionally also sparsely hirsute especially on floral parts. Buds erect. Petals bright yellow. Capsule lanceoloid, flexible, falcate, tapering gradually to a long slender sterile apex, the angles acute, contorted and twisted, the surface conspicuously wrinkled, sessile. Seeds in 1 row per locule, often becoming 2 rows toward the base of the capsule, obovoid, coarsely rugose, the surface with turgid and collapsed papillae, the raphial face with 2 small, longitudinal ridges nearly the length of the seed. Self-compatible, outcrossing. Basic chromosome number, $x = 7$.

The only species in sect. *Contortae, Oenothera xylocarpa,* is locally abundant from 2,250 to 3,050 m in open meadows, flat areas, or on slopes in loose granitic gravel, sand, or pumice. It grows in *Pinus jeffreyi* Balf. forest with *Artemisia tridentata* Nutt. or in *Pinus contorta* Dougl. ex Loud. subsp. *murrayana* (Balf.) Critchf. to *Abies magnifica* Andr. Murray forest and is known from three disjunct areas in California and adjacent Nevada: 1) Mount Rose, Washoe Co., Nevada, 2) southern Sierra Nevada, southwestern Mono Co., California, from the vicinity of Crestview south to Casa Diablo, and 3) southern Sierra Nevada, west-central Inyo and eastern Tulare counties, California, area bounded by Horseshoe and Big Whitney Meadows to the east and north, and Casa Vieja and Volcano Meadows to the south and west. The sectional name is derived from the Latin word *contortus,* twisted, in reference to the unique contorted capsules of *O. xylocarpa.*

Oenothera xylocarpa is here placed in a monotypic section because, like *O. primiveris,* most of its specialized features are not shared with any other species. Based on its lanceoloid, acutely angled capsules and relatively large seeds with papillose surface, it definitely appears to be part of the lineage that includes sects. *Ravenia, Eremia,* and *Pachylophus.* Hybrids cannot be formed in crosses with any of these species, although abortive seeds are sometimes formed in crosses between *O. xylocarpa* and *O. primiveris* or *O. maysillesii* (sect. *Oenothera* subsect. *Emersonia*). A recent study of seed anatomy (Tobe et al., in press) showed that the seeds of *O. xylocarpa* and *O. primiveris* differ from those of *O. maysillesii* primarily only in having thinner endotesta and irregularly swollen exotestal cells (papillose seed surface), but that *O. primiveris* differs further from the other two species in its thicker, 1 or 2 cell-layered exotegmen and thicker, 2–5-layered mesotesta. Cladistic analysis using general morphological characters and seed morphological characters suggests that *O. xylocarpa* probably diverged from these species relatively late in the evolution of the group and subsequently developed a number of unique derived features (Wagner et al., 1985).

OENOTHERA SECT. *LAVAUXIA*

Oenothera sect. *Lavauxia* is a distinctive section of five species. They are characterized by narrowly ovoid, ellipsoid to rhombic-obovoid capsules with oblong wings that extend essentially throughout the capsule body or triangular wings confined to the upper one-quarter to

two-thirds of the capsule. The seeds are asymmetrically cuneiform and the surface is minutely beaded. The collective range of the three North American species, *O. flava* (A. Nels.) Garrett, *O. triloba* Nutt., and *O. acutissima* W. L. Wagner, extends no further south than Guanajuato and Hidalgo, Mexico. The other two species, *O. centauriifolia* (Spach) Steud. and *O. acaulis* Cav., are disjunct in Argentina, Uruguay, and Chile. The two groups differ in features such as petal color and proportion of the capsule that is winged. The North American species have yellow petals and wings extending two-thirds or throughout the capsule length, whereas the South American species have white petals and wings extending only one-quarter to one-half the capsule length. The following subsection is proposed for the two South American species.

Oenothera L. sect. **Lavauxia** (Spach) Endl. subsect. **Australis**[3] W. L. Wagner & Dietrich, subsect. nov. TYPE: *Oenothera centauriifolia* (Spach) Steud.

Petala alba; plantae brevi-villosae; capsulae alae abrupte ad medium truncatae; intra medium carentes.

Petals white; plants short-villous, the hairs transparent to translucent, rarely creamy white, 0.1–0.4(–0.5) mm long, mixed with minute erect transparent glandular hairs, 0.1–0.2 mm long, and sparsely hirtellous, the hairs transparent to translucent, 0.7–1.7 mm long, these sometimes with a pale reddish purple pustulate base, only rarely strigillose with creamy white hairs 0.1–0.3 mm long; capsule wings abruptly truncated ⅓–½ of the way from the capsule apex, and absent or nearly so from the lower half of the capsule.

In addition to the new subsection of sect. *Lavauxia,* a nomenclatural change is needed for one of the North American taxa in this section. *Oenothera flava* occurs from Saskatchewan and Alberta, Canada, to western parts of the Great Plains, nearly throughout the Rocky Mountains to eastern Oregon and California, and south to the states of Guanajuato and Hidalgo, Mexico. Throughout most of its range it is modally autogamous, growing in seasonally moist sites or along streams; however, in montane areas of Arizona, New Mexico, and the Sierra Madre Occidental, Mexico, a large-flowered, modally outcrossing form replaces the autogamous plant. Previously these outcrossing plants had been considered a distinct species, *O. taraxacoides.* Careful study of these plants throughout their range (Wagner, unpubl.) showed that they intergrade extensively with *O. flava,* especially in Arizona near Flagstaff and throughout northern Mexico. Because of this intergradation and because it differs primarily only in flower size and breeding system, it is here treated as a subspecies of *O. flava.*

KEY TO THE SUBSPECIES OF *OENOTHERA FLAVA*

1a. Stigma elevated above or outside the ring of anthers; petals usually obcordate, (2.5–)3–4.5(–5) cm long; sepals often flecked with reddish purple splotches and with free sepal tips in bud (1.7–)2.5–10(–12) mm long; seeds over 2.5 mm long ..... subsp. *taraxacoides*

1b. Stigma surrounded by anthers; petals usually obovate with a terminal tooth, (0.7–)1–2.6(–3.8) cm long; sepals generally lacking reddish purple splotches and with free sepal tips 1–2(–5) mm long; seeds 1.8–2.2(–2.6) mm long ..... subsp. *flava*

Oenothera flava (A. Nels.) Garrett subsp. **taraxacoides** (Woot. & Standl.) W. L. Wagner, comb. et stat. nov. *Lavauxia taraxacoides* Woot. & Standl., Contr. U.S. Natl. Herb. 16: 155. 1913. TYPE: U.S.A. NEW MEXICO: Otero Co., James Canyon, Sacramento Mountains, 2,800 m, 6 July 1899, *E. O. Wooton s.n.* (US-563856, holotype, photo MO; POM, RM, isotypes). *Oenothera taraxacoides* (Woot. & Standl.) Munz, Amer. J. Bot. 17: 362. 1930.

Oenothera flava subsp. *taraxacoides* is colonial, rarely abundant in rocky clay- or sandy-loam soils of montane meadows to gravelly or sandy sites along seasonal or permanent watercourses in ponderosa pine, spruce-fir, or pine-oak forests, from three disjunct areas: 1) the Mogollon Plateau in Arizona to Catron Co., New Mexico; 2) Sacramento Mountains and Sierra Blanca, Lincoln and Otero counties, New Mexico; and 3) the Sierra Madre Occidental from northern Chihuahua south to Durango, Mexico.

[3] Treatment of this new subsection in collaboration with W. Dietrich, Botanisches Institut der Universität, Universitätsstrasse 1, D-4000, Düsseldorf 1, Germany.

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STUDIES IN THE ARALIACEAE OF NICARAGUA, AND A NEW WIDESPREAD SPECIES OF *OREOPANAX*[1]

M. J. Cannon and J. F. M. Cannon[2]

Abstract

New information on the Araliaceae arising from the preparation of an account of the family for the *Flora de Nicaragua* is reviewed in the wider context of studies for the *Flora Mesoamericana,* and **Oreopanax nicaraguensis** is described.

During the preparation of an account of the Araliaceae for the forthcoming *Flora de Nicaragua* we have encountered a number of problems, but as the concise format of that work prevents their wider discussion, some explanatory notes are presented here together with the description of a new species. These decisions were taken in the context of a broader study of the family in Central America, and this will appear in due course in *Flora Mesoamericana.*

Oreopanax Decne & Planch.

The considerable difficulties in separating the entire-leaved species of *Oreopanax* have been noted by various authors, notably A. C. Smith (1936) and L. O. Williams (1966). In Nicaragua, the entire-leaved specimens are easily divided into two groups, one of which is referable to *O. capitatus* (Jacq.) Decne & Planch., which, in our opinion, must also include *O. liebmannii* Marchal. The other appears to be a new species, here described as *O. nicaraguensis*. *Oreopanax liebmannii* has generally been separated from *O. capitatus* on the basis of its narrow leaves and smaller staminate and hermaphrodite capitula, but it has proved quite impossible to maintain this distinction in our area, there being a complete range in leaf shape and capitulum size. *Oreopanax capitatus* has a very wide distribution from Mexico to Brazil and the West Indies and A. C. Smith (1936) has drawn attention to the difficulty of separating *O. liebmannii* in the southern part of its range (Costa Rica and Panama), and throws doubts upon its specific status. We are in complete agreement with this view and include *O. liebmannii* within the synonymy of *O. capitatus*.

Marchal cited specimens of *O. liebmannii* from Copenhagen in his original description, together with others from Paris and Leningrad. There are two sheets of *Liebmann no. 14* at Copenhagen, one of which has two separate branches, one bearing staminate heads, the other hermaphrodite heads, with the locality recorded as Donguia (a probable misspelling for Donaguia in Mexico). We designate this as the lectotype. The other sheet from Donaguia bears a staminate branch, while packets hold part of a hermaphrodite inflorescence and several leaves. A third sheet from Copenhagen bears a specimen of a staminate inflorescence labelled *no. 11,* and three separate leaves, one of which is labelled *no. 12*. One leaf closely resembles those of Liebmann *no. 11* from Donguia and probably has been incorrectly mounted on this sheet. The flowering branch (*no. 11*) on this sheet does not match the Donguia specimens very closely, whereas the other two leaves may be from another species. The locality for *no. 11* on this sheet is quoted as '?' and that for *no. 12* is Alpatlahua. The specimen from Paris, *Hahn* from 'Forêt de Perote', is a staminate branch that does not resemble the Donguia specimens very closely; we have not seen the sheet from Leningrad.

All the specimens of *Oreopanax* we have seen from Nicaragua with palmately lobed leaves are referable to *O. geminatus* Marchal. Comparison of type material of *O. geminatus* with *O. lachnocephalus* Standley and with other specimens from Honduras shows many similarities. These species have been separated mainly by the presence or absence of peduncles, but examination of the type material of the former (*Oersted no. 7* from Segovia, Nicaragua), which is preserved at Copenhagen, disclosed the presence of a few pedunculate capitula. We therefore propose the inclusion of *O. lachnocephalus* within *O. gemi-*

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natus, thus confirming the tentative suggestion made by L. O. Williams (1966). A new species of *Oreopanax* is described here from Nicaragua. It has also been found to the south of our area in Costa Rica and Panama, but, as yet, has not been collected in Guatemala or Honduras. The *Oreopanax* species of Nicaragua can be separated by the following key:

1a. Leaves digitate, inflorescence racemose ..... *O. xalapensis* (Kunth) Decne & Planch.
1b. Leaves simple, entire or lobed, inflorescence paniculate or compound umbellate.
2a. Leaves 5–7 lobed, styles of hermaphrodite flowers 2 ..... *O. geminatus* Marchal
2b. Leaves entire, styles of hermaphrodite flowers 5–12.
3a. Peduncles glabrous, leaf bases obtuse to cordate, disc fleshy, forming a cup ..... *O. nicaraguensis* M. J. Cannon & J. F. M. Cannon
3b. Peduncles often puberulent, leaf bases acute to rounded, disc neither fleshy nor forming a cup ..... *O. capitatus* (Jacq.) Decne & Planch.

Oreopanax nicaraguensis M. J. Cannon & J. F. M. Cannon, sp. nov. TYPE: NICARAGUA. DEPT. DE JINOTEGA: Camino a Aranjuez, Santa Elena, 13°01′24″N, 85°54′57″W, alt. ca. 400 m. Arbol 40 m de alto frutos morados, Nov. 1983. Hermaphrodite inflorescence, *Vega & Quezada 197* (holotype, BM; isotypes, HNMN, MO). Figures 1, 2.

Oreopanax capitato (Jacq.) Decne & Planch. affinis, sed foliis latissimis, venatione 5–7 nervia, stylis in cupula insertis, differt, *O. obtusifolio* L. Williams accedens, sed foliis supra nitidis, apice acuminatis, stylis in cupula insertis, inflorescentia compactissima, fructibus majoribus, distinguenda. Arbor ad 40 m alta, rare scandens, omnio glabra vel inflorescentia tantum pubescens, pilis stellatis sessilibus longe ramosis. Folia simplicia, laminis 7–16 × 7–14 cm, suborbicularis vel late ovatis vel rhombo-ovatis, apice acuminatis acumine brevi, plus minusque rotundato vel acuto, basi rotundatis vel cordatis, e basi conspicue (3–)5–7(–9) nervis, coriaceis, supra saepe nitidis; petiolus 4–15 cm longus, striatus, basi paulum incrassatus. Inflorescentia mascula plus minusque umbellata vel paniculata, bracteis infraramis 2–3(–10) cm longis cuspidatis, vel nullis, ramis pedunculisque striatis, glabris vel stellato-pubescentibus, pedunculis 4–8 mm longis, crassis, bracteis subpedunculis 2–4 mm longis, latissime ovatis, breve cuspidatis; capitulum ad 5 mm diametro, subglobosum, bracteis suborbicularis; calyx obconicus, limbo late lobato vel undulato; petali 1.5 mm longi, deltoidei; stamina filamento 1.5 mm longo, anthere 1.5 mm longo, oblongo; stylus 1. Inflorescentia fructifera compactis, plerumque plus minusque umbellatis rarissime paniculatis, ramis 4–6 cm longis, pedunculis 5–20 mm longis, crassis, bracteis subpedunculis ad 3 mm longis apice acutio. Fructus 6–10 × 4–6 mm, ovoideus vel subglobosus, carnosus, 2–5(–8) in quoque capitulo, bracteis subfructibus 5–8 mm longis, suborbicularis, ab initio ciliatis sub maturitatione emarginatus et marginis suberosis; discus carnosus urceolatus; styli (6–)7(–9), 2–3 mm longi, in cupula inserti, liberi vel basi crassi et contigui, apice arcuato reflexi. Semina albumine ruminato.

Trees to 40 m tall, or rarely vines, glabrous throughout or the inflorescence only pubescent, the hairs stellate, sessile, long-branched. Leaves entire, blade 7–16 × 7–14 cm, suborbicular to broadly ovate or rhomboid ovate, tip with a short more or less rounded or acute acumen, base rounded to cordate, conspicuously (3–)5–7(–9)-nerved from the base, coreaceous, upper surface shiny; petioles 4–15 cm long, striate, somewhat swollen at the base. Staminate inflorescence more or less umbellate or paniculate, bracts subtending branches 2–3(–10) mm, cuspidate or absent, branches and peduncles striate, glabrous or stellate pubescent, peduncles 4–8 mm long, stout, bracts subtending peduncles 2–4 mm long, very broadly ovate, shortly cuspidate, heads to 5 mm diam., subglobose, bracts sub-orbicular; calyx obconic, limb broadly lobed or undulate; petals 1.5 mm long, deltoid; filaments 1.5 mm long, anthers 1.5 mm long, oblong; styles 1. Fruiting inflorescence compact, usually more or less umbellate, very rarely paniculate, branches 4–6 cm long, peduncles 5–20 mm long, stout, bracts subtending peduncles to 3 mm, apex acute. Fruits 6–10 × 4–6 mm, ovoid to subglobose, fleshy, 2–5(–8) per head, bracts subtending fruits 5–8 mm long, suborbicular, at first ciliate, emarginate and cork-edged when mature; disc fleshy, urceolate, styles 2–3 mm long within a cup, (6–)7(–9), free or swollen and touching at the base, the apices arcuate-reflexed. Endosperm ruminate.

The new species differs from the common and widespread *O. capitatus* (Jacq.) Decne & Planch. by its very broad leaves, the leaf venation, the styles within a cup-shaped hollow at the apex of the fruit, and its compact, large-fruited inflorescence. It differs from *O. obtusifolius* L. Williams by the shiny upper leaf surface, the acuminate leaf apices, the styles within the cup-shaped hollow and the larger fruited, more compact inflorescence. While *O. obtusifolius* seems to be found to the north of the region in Mexico, Belize, Guatemala and Honduras, *O. nicaraguensis* appears to have a more southerly distribution in Nicaragua, Costa Rica, and Panama.

FIGURE 1. *Oreopanax nicaraguensis*, holotype, showing fruits, *Vega & Quezada 197* (BM).

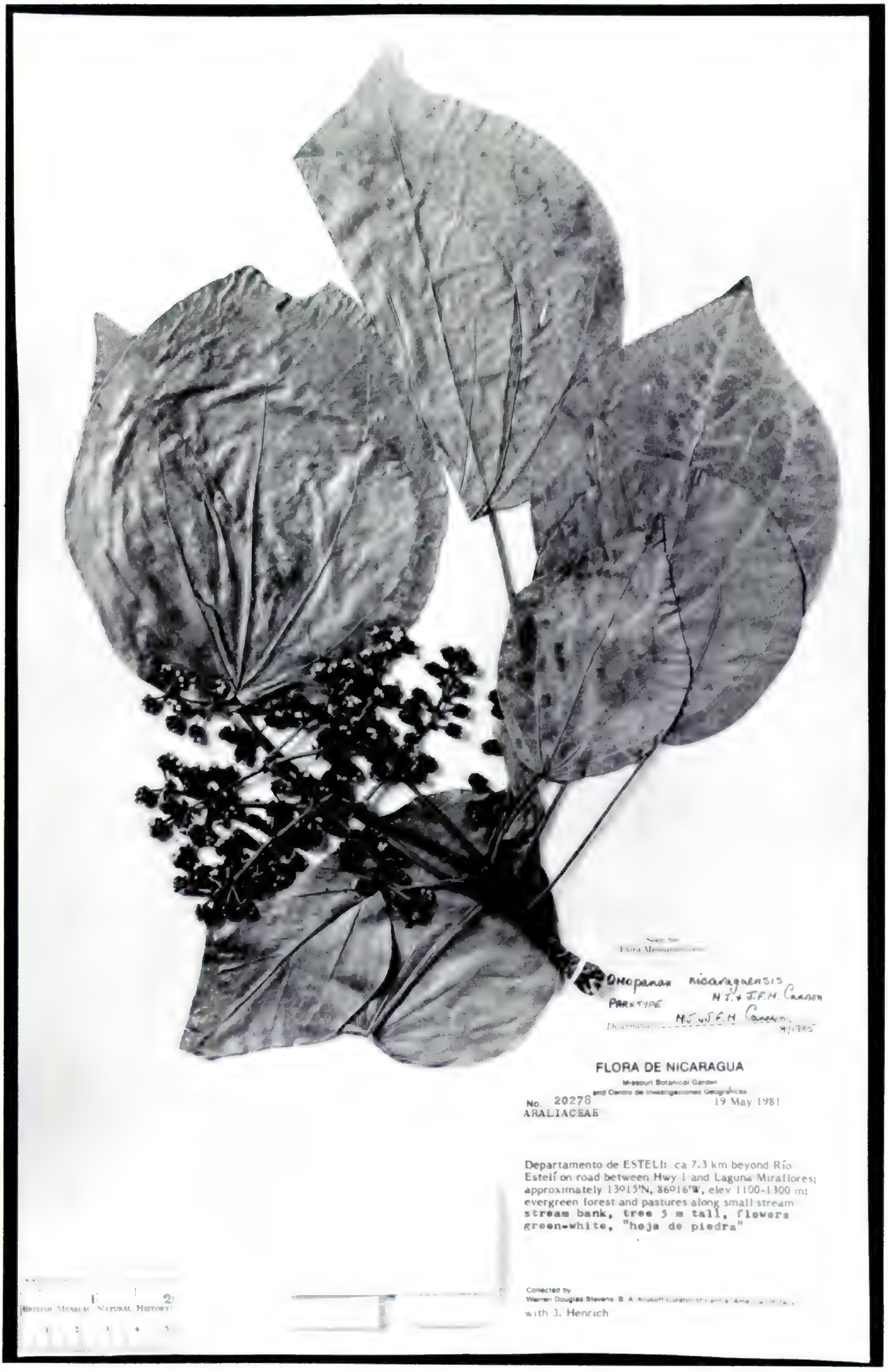

FIGURE 2. *Oreopanax nicaraguensis*, paratype, showing flowers, *Stevens & Henrich 20278* (BM).

Paratypes: NICARAGUA. ESTELI: ca. 7.3 km beyond Rio Esteli on road between Highway 1 and Laguna de Miraflores, ca. 13°15′N, 86°16′W, alt. 1,100–1,300 m. 19 May 1981. Male inflorescence. *Stevens & Henrich 20278* (BM, HNMN, MO); El Tisey, 1,500 m, *Laguna 292* (BM, HNMN). JINOTEGA: Sanatorio Aranjuez, 1,300–1,350 m, *Sandino & Martinez 4328* (BM, HNMN, MO). MATAGALPA: Cerro El Picacho, 1,420–1,520 m, *Stevens 22123* (BM, MO). MADRÍZ: Cerro Arenal, 1,500 m, *Atwood & Neill 274* (HNMN, MO). ZELAYA: Comarca Waslala 520–560 m, *Moreno 17261* (BM, HNMN).

COSTA RICA. LIMÓN: Chiripo National Park, 2,800 m, *Garwood, Gibby, Hampshire & Humphries 1332* (BM). SAN JOSÉ/CARTEGO: Cordillera de Talamanca, Cerros Cuerici, 3,160 m, *Davidse 24705* (BM, MO). HEREDIA: San Isidro, Conceptión, 1,450 m, *Khan, Tebbs & Vickery 1270* (BM, HNMN). ALAJUELA: Monte verde, Cordillera de Tilaran, 1,500–1,560 m, *Dryer 1360* (F).

PANAMA. CHIRIQUÍ: Boquete, 2,900–2,950 m, *Croat 34885* (BM, MO).

SCHEFFLERA J. R. & G. A. FORST.

The northern limit of this genus in Central America occurs in Nicaragua, with the sole exception of *S. morototoni* (Aubl.) Maguire, Steyermark & Frodin, which, until recently, was included in the genus *Didymopanax*. However, that genus is indistinguishable from *Schefflera* other than by stigma number, which is itself variable, even within one plant, as has been clearly established by Frodin (pers. comm.) in a wide ranging survey of *Schefflera* and related groups. *Schefflera nicaraguense* (Standley) A. C. Smith was described from Nicaragua and has now been found also in Costa Rica. A further, apparently undescribed, species of *Schefflera* has been collected in the Department of Rio San Juan in southern Nicaragua: Río Indio, 5.5 hours up river from San Juan del Norte (25 Hp) 11°07′N, 83°50–52′W, alt. less than 20 m, Finca las Delicias de Alfonso Crespo Aragon, 8 Sept. 1982. *Riviere 292* (MO).

This species is epiphytic, with about 10 leaflets, 22–23 × 6.5 cm, oblong-lanceolate, glabrous, tips acuminate (acumen 1 cm), bases acute to rounded, lateral veins 10–12, petiolules 9–11 cm long, terete. Petiole and ligule not seen. Inflorescence at least 6-, probably many, branched, ferruginous pubescent, bracts subtending branches 1–2 mm long, truncate, branches ca. 30 cm long, striate; peduncles slender, 6–8 mm long, ebracteate just after anthesis; pedicels very slender, 3–4 mm, (4–)5 per umbel; calyx teeth cuspidate; calyptra very pointed and cuspidate at the apex, densely ferruginous pubescent. Stylar cone of very young fruit 1–2 mm long, styles 5, becoming free above for about half of their length. It may be related to the very variable species *Schefflera systyla* (Donn. Smith) Viguier from Costa Rica and Panama, from which it seems to differ by its many-branched inflorescence, its very slender pedicels and peduncles, and its densely pubescent calyptra. The inflorescence somewhat resembles that of *S. sphaerocoma* Harms from South America, but the leaflets differ greatly in shape and venation.

Although by the standards of this difficult and complex genus, this taxon seems relatively distinct, we do not propose to give it formal recognition at this time, as the single known specimen is both immature and seriously incomplete, and the purposes of Science will be better served by waiting until further material is available for consideration, leading perhaps to the designation of a more representative type specimen.

We are grateful to Prof. David Frodin for discussion of the *Schefflera* problems in the light of his very extensive long-term monographic studies on the genus.

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NOTES

CHROMOSOME NUMBERS OF NEW CALEDONIAN PLANTS

Chromosome numbers of 26 collections that represent first reports for 23 species embracing 17 families of New Caledonian flowering plants are presented and discussed. Chromosome numbers are documented for the first time in the genera *Adenodaphne* (n = 12), *Agatea* (n = 8), *Dubouzetia* (n = ca. 90), *Kibariopsis* (n = 19), *Montrouziera* (n = ca. 29), *Oncotheca* (n = 25), *Phelline* (n = 17), and *Sphenostemon* (n = ca. 26). Two of these represent the first reports for Oncothecaceae and Sphenostemonaceae. Numbers not previously reported are established in *Belliolum* (n = ca. 43), *Garcinia* (n = 33), *Grevillea* (n = ca. 22), and *Zygogynum* (n = ca. 43).

Although the flora of New Caledonia is one of great potential value in the interpretation of phytogeographic and phylogenetic relationships, few species are cytologically known. In an effort to contribute to a better understanding of these relationships, the Missouri Botanical Garden included as part of its 5-year-long field program on the island the collection of flower buds for cytological study. The purpose of this paper is to present and discuss the 26 chromosome counts that these collections have yielded so far.

Materials and Methods

Floral buds for study were preserved and stored in modified Carnoy's fixative (6 chloroform : 3 absolute ethanol : 1 glacial acetic acid; v:v:v). Meiotic, and in two cases, mitotic chromosome determinations were made from anther material macerated in acetocarmine. Hoyer's solution (Beeks, 1955) was added to the preparations in order to increase quality and durability. The indexes of chromosome numbers that were consulted for interpretive and comparative data include Fedorov (1974), Goldblatt (1981, 1984), and Moore (1973, 1974, 1977). The sequence of families in the list follows Cronquist (1981). All collection numbers (Table 1) are G. McPherson's. Voucher specimens are deposited at MO.

Results

The results are presented in Table 1. Where there was some question about the cytological determination due to small size of chromosomes, high numbers, inadequate fixation, or stickiness, the number reported is listed as approximate (prefaced with ca.). These are the reports in greatest need of additional confirmation. There were no clear indications of meiotic abnormalities in any of the material studied.

Discussion

Winteraceae. The report here of n = ca. 43 (Table 1) for *Belliolum crassifolium* is the second for this species and differs from the earlier record of n = ca. 86 (Ehrendorfer et al., 1968). Our determination of n = ca. 43 for *Zygogynum pomiferum* subsp. *balansae* is also a lower ploidy level than previously known in this New Caledonian endemic genus. The only other report available is n = 86 for *Z. baillonii* V. Tiegh. (Ehrendorfer et al., 1968).

Monimiaceae. *Hedycarya parvifolia* has n = 19 (Table 1), a number that has also been reported in two other species of the genus (Ehrendorfer et al., 1968). Hair and Beuzenberg (1959) have recorded n = 57 in a third species of *Hedycarya*. The report here of n = 19 for *Kibariopsis caledonica* is the first for this endemic New Caledonian genus. This number has now been established in at least five genera of Monimiaceae.

Lauraceae. The count here of n = 12 for *Adenodaphne uniflora* apparently represents the first report for this genus. The same number characterizes many genera of the family.

Chloranthaceae. The report here of n = ca. 14 for *Ascarina rubricaulis* agrees with an earlier one of $2n$ = 28 (Ehrendorfer et al., 1968). This number is also known in *Chloranthus* (Sugiura, 1931).

Fagaceae. The count of n = 13 for *Nothofagus discoidea* (Table 1) is the same as that found in all seven species of the genus already investigated (Armstrong & Wylie, 1965; Ono, 1977). Other genera in Fagaceae reportedly have n = 11, 12, and 24.

Oncothecaceae. The report of n = 25 for *Oncotheca balansae* (Table 1) is the first for this endemic New Caledonian family. At diakinesis ring pairs of chromosomes ranged from about 1.5–2 μm in diameter while rod pairs ranged from about 2–3.3 μm in length. The inclusion of On-

TABLE 1. Chromosome numbers of New Caledonian plants.

Taxon	*N*	2*n*	Collection data
Winteraceae			
Belliolum crassifolium (Baillon) van Tieghem	ca. 43		Thy Valley, *1852*
Zygogynum pomiferum Baillon subsp. *balansae* (van Tieghem) Vink[a]	ca. 43		Mt. Dzumac, *3880*
Monimiaceae			
Hedycarya parvifolia Perk. & Schltr.[a]	19		Mt. Do, *2000*
Kibariopsis caledonica (Guillaumin) Jérémie[b]	19		Mandjélia, *2546*
Lauraceae			
Adenodaphne uniflora (Guillaumin) Kostermans[b]	12		Yaté Dam, *3886*
Chloranthaceae			
Ascarina rubricaulis Solms	ca. 14		Plaine des Lacs, *4612*
Fagaceae			
Nothofagus discoidea (Baum.-Bodenh.) van Steenis[a]	13		Thy Valley, *2487*
Oncothecaceae[c]			
Oncotheca balansae Baillon[b]	25		Thy Valley, *3130, 3301*
Clusiaceae			
Garcinia puat (Montrouzier) Guillaumin[a]	33		Mt. Mé Ori, *2013*
Montrouziera sphaeroidea Pancher ex Planch. & Triana[b]	ca. 29		Plaine des Lacs, *3014*
Elaeocarpaceae			
Elaeocarpus speciosus Brongn. & Gris[a]		30	Mt. Mé Maoya, *2950*
Dubouzetia elegans Brongn. & Gris[b]	ca. 90		Mt. Mé Ori, *3029*
Violaceae			
Agatea sp.[b]	8		Rivière Bleue Valley, *3670*
Symplocaceae			
Symplocos baptica Brongn. & Gris[a]	11		Mt. Do, *3810*
Pittosporaceae			
Pittosporum cf. *dzumacense* Guillaumin[a]	12		Mt. Do, *3813*
Proteaceae			
Beauprea neglecta R. Virot[a]	11		Houailou, *3261*
Grevillea meisneri Montrouzier[a]	ca. 22		Népoui Valley, *1896*
Olacaceae			
Olax hypoleuca Baillon[a]	12	24	Goro, *3631*
Aquifoliaceae			
Phelline sp.[b]	17		Mt. Mé Ori, *3041*
Phelline sp.[b]	17		Col de Mouirange, *3599*
Sphenostemonaceae[c]			
Sphenostemon comptonii Baker f.[b]	ca. 26		Mt. Mé Ori, *3047*
Malpighiaceae			
Acridocarpus austrocaledonicus Baillon[a]	9		Tiébaghi, *3306*
Apocynaceae			
Alstonia plumosa Labill.[a]	11		Thy Valley, *1877*
A. vieillardii van Heurck & Muell. Arg.[a]	11		Montagne des Sources, *1640*
Rauvolfia semperflorens (Muell. Arg.) Schlechter[a]	11		Mt. Mou, *1871*

[a] Denotes species not recorded in chromosome indexes.
[b] Denotes genera not recorded in chromosome indexes.
[c] Denotes families not recorded in chromosome indexes.

cothecaceae in Theales by Cronquist (1981) is compatible with cytological data because $n = 25$ is also known in *Ternstroemia* (Theaceae) (Morinaga & Fukushima, 1931).

Clusiaceae. The count of $n = 33$ for *Garcinia puat* (Table 1) is unique in the genus. However, $n = 22$, 24, ca. 27, ca. 28, ca. 29, 36, 38, 40, and 48 have been reported for *Garcinia* (cf. Fedorov, 1974; Goldblatt, 1984). The count of $n =$ ca. 29 for *Montrouziera sphaeroidea* (Table 1) apparently represents the first for this endemic New Caledonian genus. In addition to the numbers listed above for *Garcinia*, $n = 28$ and ca. 28 have been reported for *Allanblackia* (Mangenot & Mangenot, 1957) and *Pentadesma* (Mangenot & Mangenot, 1962), respectively.

Elaeocarpaceae. The count of $2n = 30$ for *Elaeocarpus speciosus* (Table 1) agrees with reports for at least three other species of the genus (Mehra, 1976; Rattenbury, 1957). Other numbers reported for *Elaeocarpus* are $n = 12$ and $n = 14$ (Arora, 1961; Ono, 1975). Our report of $n =$ ca. 90 for *Dubouzetia elegans* is apparently the first for this genus. This number may represent dodecaploidy based on $n = 15$.

Violaceae. The report here for *Agatea* of $n = 8$ is the first for the genus. It agrees with reports for *Hybanthus*, *Ionidium*, and a couple of species of *Viola* (Moore, 1973, 1974; Goldblatt, 1981, 1984). Two species of the Hawaiian endemic genus *Isodendrion* also have $n = 8$ (Carr, 1985).

Symplocaceae. The count of $n = 11$ for *Symplocos baptica* (Table 1) agrees with the number established in several other species in the genus. Counts of $n = 12$ (Nevling, 1969) and $2n =$ ca. 90 (Nooteboom, 1975) have also been reported for *Symplocos*.

Pittosporaceae. The first report here of $n = 12$ for *Pittosporum* cf. *dzumacense* agrees with nearly every report for the family. Only *Citriobatus* differs by having $n = 18$ (Fedorov, 1974).

Proteaceae. The count of $n = 11$ for *Beauprea neglecta* (Table 1) accords with the report for *B. paniculata* Brongn. & Gris. (Johnson & Briggs, 1963), the only other count for the genus. Counts of $n = 11$ are common in Proteaceae, but $n = 22$ has not been reported previously. Thus, the count of $n =$ ca. 22 given here for *Grevillea meisneri* is noteworthy, but needs verification. In any case, it contrasts markedly with $n = 10$, the only other number known in the approximately 27 species of *Grevillea* that have been investigated (cf. Fedorov, 1974).

Olacaceae. The count of $n = 12$ for *Olax hypoleuca* (Table 1) agrees with the only other report available for the genus. *Olax nana* Wall. and *Schoepfia fragrans* Wall. appear to be the only other species in the family reported to have $n = 12$ (Mehra, 1976).

Aquifoliaceae. The report here of $n = 17$ for two collections of *Phelline* represent the first for this genus. The same number has also been reported in a few species of *Ilex*, including *I. matanoana* and *I. mertensii* (Ono & Masuda, 1981).

Sphenostemonaceae. Our count of $n =$ ca. 26 for *Sphenostemon comptonii* is apparently the first for this family. At diakinesis ring pairs of chromosomes ranged from about 2.3–3.4 μm in diameter while rod pairs were about 3 μm long. Historically, the family has been included in Trimeniaceae, Clusiaceae, Aquifoliaceae, or Theaceae. Cronquist (1981) included *Sphenostemon* in the Aquifoliaceae. However, strictly in terms of chromosome numbers, the greatest accord appears to be with Theaceae (cf. *Ternstroemia japonica*, $n = 25$; Morinaga & Fukushima, 1931) or Clusiaceae, but obviously the data are equivocal.

Malpighiaceae. *Acridocarpus austrocaledonicus* is here reported to have $n = 9$. This number has also been reported for the two other species in the genus that are known cytologically (Mangenot & Mangenot, 1962). *Tristellateia* and *Stigmaphyllon* appear to be the only other genera of Malpighiaceae reported to have species with this number (Fedorov, 1974).

Apocynaceae. First reports of $n = 11$ are given here for *Alstonia plumosa* and *A. vieillardii*. This number and $n = 22$ and 44 have also been found in other species of the genus (Fedorov, 1974). A first report here of $n = 11$ for *Rauvolfia semperflorens* agrees with the number in several other species in *Rauvolfia*, in which $n = 22$, 33, 44, and 88 are also known (Fedorov, 1974; Goldblatt, 1981).

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A NEW COMBINATION IN *LUDWIGIA* SECT. *MICROCARPIUM* (ONAGRACEAE)

The following new combination is proposed in advance of ongoing monographic studies of North American *Ludwigia* in order to make the name available for numerous floristic projects and for a biosystematic study of *Ludwigia* sect. *Microcarpium* (Peng, 1987). It will be discussed and justified in my subsequent publication, and is offered at this time with minimal synonymy.

Ludwigia glandulosa Walter subsp. **brachycarpa** (Torrey & A. Gray) Peng, comb. nov. *L. cylindrica* Elliott β. *brachycarpa* Torrey & A. Gray, Fl. N. Amer. 1: 524. 1840 non *Jussiaea brachycarpa* Lam., Encycl. 3: 331. 1789. *L. glandulosa* Walter var. *torreyi* Munz, Bull. Torrey Bot. Club 71: 164. 1944, illeg. subst. LECTOTYPE: U.S.A. Texas: Austin Co., San Felipe, "third collection," 1833–1834, *T. Drummond 84* [GH; isolectotypes, GOET, K (2 sheets), W; here designated].

Munz (1944) renamed this taxon because he thought that Torrey and Gray (1840) based it on *Jussiaea brachycarpa* Lam. (= *L. glandulosa* Walter subsp. *glandulosa*), which, however, is doubtful. In any case, they were free to use the same epithet for a variety, so that "*brachycarpa*" has priority at the varietal level. Here I am taking it up for the short-fruited, western subspecies of *Ludwigia glandulosa*. Munz (1944) chose a lectotype for this entity (*Hall 219*, from Hempstead, Waller Co., Texas) that was not collected until more than 30 years after Torrey and Gray wrote; his choice must therefore be disregarded. Of the two specimens they cited, only the lectotype I have chosen meets the criteria of this entity as we now understand it, having short mature fruits. In this respect it agrees more fully with Torrey and Gray's diagnosis. Chapman's collection (no. 38) from middle Florida, without definite locality (GH, NY), is an immature specimen of subsp. *glandulosa*, which Torrey and Gray considered to be their short-fruited variety.

Ludwigia glandulosa subsp. *brachycarpa* differs from the subsp. *glandulosa* in its smaller stature, narrower leaves, and smaller flowers and capsules. In addition, the seed surface pattern of these two entities—a feature that is often diagnostic in *Ludwigia* sect. *Microcarpium*—is sharply distinct. In *L. glandulosa* subsp. *glandulosa*, the cells are longitudinally elongate, whereas in subsp. *brachycarpa*, they are transversely elongate.

Ludwigia glandulosa subsp. *brachycarpa* occurs along the Gulf Coast from extreme southwestern Louisiana to Nueces County, Texas, and northward through eastern Texas to southcentral Oklahoma. Subspecies *glandulosa*, in contrast, has a much broader distributional range: it occurs throughout the Atlantic and Gulf Coastal Plains and the Mississippi Embayment, westward to eastern Texas and southeastern Oklahoma.

Ludwigia glandulosa subsp. *brachycarpa* thus has a range that lies along the western edge of that of the subsp. *glandulosa* in northern Texas and Oklahoma. It grows in the same areas as subsp. *glandulosa* throughout much of its range, but extends farther south and west. The distinctiveness of these two subspecies is probably maintained by self-pollination.

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DESCRIPTION OF A NEW SECTION AND SUBSECTION IN *CLARKIA* (ONAGRACEAE)

In their monograph of *Clarkia*, Lewis and Lewis (1955) described two new sections in the genus, sects. *Peripetasma* and *Fibula*. In addition, they described four subsections under *C.* sect. *Peripetasma*: subsects. *Peripetasma*, *Lautiflorae*, *Micranthae*, and *Prognatae*. The type of both *C.* sect. *Peripetasma* and *C.* subsect. *Peripetasma* is *Godetia bottae* Spach [≡ *C. bottae* (Spach) Lewis & Lewis]. The type of *C.* sect. *Fibula* is *Godetia deflexa* Jepson [≡ *C. deflexa* (Jepson) Lewis & Lewis].

Raven and Parnell (1977) re-examined the type of *Godetia bottae* and concluded that it is conspecific with the type of *G. deflexa*. Because *G. bottae* has priority over *G. deflexa* (1835 versus 1907), the correct name for the taxon Lewis and Lewis (1955) treated as *Clarkia deflexa* is *Clarkia bottae*. In addition, the taxon treated as *C. bottae* by Lewis and Lewis was provided with a new name, *Clarkia lewisii* Raven & Parnell, since no other specific epithet was available.

Further nomenclatural adjustments must result from the work of Raven and Parnell (1977). Article 10.1 of the International Code of Botanical Nomenclature (ICBN) provides that "the type of a name of any subdivision of a genus is the type of a name of a species . . . for purposes of designation or citation of a type, the species name alone suffices . . . ." Thus, Raven and Parnell's investigation demonstrated that the type of *Clarkia* sect. *Peripetasma*, which is also the type of *C.* subsect. *Peripetasma*, and the type of *Clarkia* sect. *Fibula* are conspecific. Since "the application of names of taxa of the rank of family or below is determined by means of nomenclatural types . . . ." (ICBN, Art. 7.1), the description accompanying the publication of *C.* sect. *Peripetasma* and *C.* subsect. *Peripetasma* is simply in error insofar as it does not apply to the taxon including the type of *C. bottae*; *C.* sect. *Fibula* and *C.* sect. *Peripetasma* are taxonomic synonyms; and the section and subsection including *C. lewisii* are without a name.

Article 57.2 (ICBN) provides that if two taxa bearing names of equal priority are united, as we propose to unite *Clarkia* sect. *Fibula* and *C.* sect. *Peripetasma*, one of them must be chosen, and the choice must be followed by subsequent workers. In the interests of nomenclatural stability we choose *C.* sect. *Fibula* as the name for the section including the types of *C. deflexa* and *C. bottae*. In addition, we describe a new section and subsection to accommodate those taxa that Lewis and Lewis (1955) included in *C.* sect. *Peripetasma* and *C.* subsect. *Peripetasma*. A synopsis of the taxa involved is provided below.

Clarkia Pursh sect. **Fibula** Lewis & Lewis, Univ. Calif. Publ. Bot. 20: 333. 1955. TYPE: *Godetia deflexa* Jepson, Univ. Calif. Publ. Bot. 2: 332. 1907. [≡ *C. deflexa* (Jepson) Lewis & Lewis, = *C. bottae* (Spach) Lewis & Lewis]

Clarkia Pursh sect. *Peripetasma* Lewis & Lewis, Univ. Calif. Publ. Bot. 20: 313. 1955. *Clarkia* Pursh subsect. *Peripetasma* Lewis & Lewis, Univ. Calif. Publ. Bot. 20: 315. 1955. TYPE: *Godetia bottae* Spach, Nouv. Ann. Mus. Hist. Nat. 4: 393, 1835. [≡ *C. bottae* (Spach) Lewis & Lewis]

Erect herbs; stems glabrous and glaucous; rachis of the inflorescence erect; buds deflexed, becoming erect as the flowers open; floral tube obconical, 2–3 mm long, the ring of hairs at the apex; sepals remaining united and deflexed to one side at anthesis; petals fan-shaped, 1–3 cm long, flecked, the claw very short or obscure; stamens 8, in two series, the inner usually with cream-colored pollen, the outer at first divergent, the pollen blue; anthers obtuse, shorter than the filaments; filaments slender; immature capsule terete or 4-grooved.

1. **Clarkia bottae** (Spach) Lewis & Lewis, Madroño 12: 33. 1953. *Godetia bottae* Spach, Nouv. Ann. Mus. Hist. Nat. 4: 393. 1835. *Oenothera godetia* Steudel, Nomencl. Bot., 2nd edition, 2: 206. 1841, nom. illeg. TYPE: U.S.A. California: s.d., *Paolo Emilio Botta s.n.* (P; fragment, DS).

   Godetia deflexa Jepson, Univ. Calif. Publ. Bot. 2: 332. 1907. *Godetia bottae* var. *deflexa* (Jepson) Hitchcock, Bot. Gaz. (Crawfordsville) 89: 355. 1930. *Clarkia deflexa* (Jepson) Lewis & Lewis, Madroño 12: 33. 1953. TYPE: U.S.A. California: sandy plains of Los Angeles, 1854, *Lobb s.n.* (K).

2. **Clarkia jolonensis** Parnell, Madroño 20: 322. 1970. TYPE: U.S.A. California: Monterey Co., 9 mi. NW of Bradley along Jolon road, 3

June 1963, *Thorne & Everett 32186* (holotype, LA; isotype, CAS).

Clarkia Pursh sect. **Sympherica** Holsinger & Lewis, sect. nov. TYPE: *Clarkia lewisii* Raven & Parnell, Ann. Missouri Bot. Gard. 64: 642. 1977 [1978].

Herbae erectae; caulibus pubescentibus raro subglabris; inflorescentium axe in apice recurvato; calycis tubo obconico, 0.5–5 mm longo, annulo pilorum ad apicem interdum in medio ornato; calycis limbo sub anthesi connato et declinato; petalis 5–35 mm longis, oblanceolatis vel obovatis vel flabelliformis interdum bilobis, plerumque ferme purpureopunctulatis, unguiculis brevis, staminibus 8, circilis duo dissimilibus; antheris obtusis quam filamenta brevioribus, filamentis gracilibus; ovario 4- vel 8-canaliculato vel 8-costato.

Erect herbs; stems puberulent, at least above, with short upwardly curled hairs, rarely glabrate; rachis of the inflorescence recurved in bud, the buds pendulous; floral tube obconical, 0.5–5 mm long, the ring of hairs at the middle or more frequently at or near the apex; sepals remaining united and deflexed to one side at anthesis; petals 5–35 mm long, oblanceolate to obovate or fan-shaped, sometimes bilobed, usually flecked with reddish purple, the claw short or obscure; stamens 8, in two series, the inner usually with cream-colored pollen, the outer with blue pollen; anthers obtuse, shorter than the filaments; filaments slender; immature capsule 4- or 8-grooved or 8-ribbed.

The name for this section is taken from the Greek, *συμφέρων* (useful) and the adjectival suffix *-ικου* (fitness or ability), referring to the usefulness this group has had in several evolutionary studies. The results of a comparison of *Clarkia lingulata* Lewis & Lewis and *Clarkia biloba* (Durand) Nelson & Macbride using the techniques of enzyme electrophoresis (Gottlieb, 1974) were consistent with the hypothesis that *C. lingulata* is a recent derivative of *C. biloba* (Lewis & Roberts, 1956; Lewis, 1962). All of the diploid members of this section, with the exception of *C. rostrata* Davis, have two loci coding for subunits of the cytosolic isozyme of phosphoglucoisomerase (PGI) instead of only one locus, as is characteristic of most diploid plants (Gottlieb, 1982). This is also the only section in *Clarkia* in which there are differences between species in the number of loci coding for cytosolic PGI (Gottlieb & Weeden, 1979). Four of the eight diploid species in this section have only one locus coding for subunits of the cytosolic isozyme of 6-phosphogluconate dehydrogenase (6PGD), while the remainder of the diploid species in the genus have two loci coding for cytosolic 6PGD. In addition, two of the diploid species in this section have only one locus coding for subunits of the plastid 6PGD, while other species in the genus have two loci coding for plastid 6PGD (Odrzykoski & Gottlieb, 1984). Finally, a recent analysis based on restriction mapping of chloroplast DNA indicates that *Heterogaura heterandra* (Torrey) Coville and *Clarkia dudleyana* (Abrams) Macbride are more closely related to one another than either is to any other extant species (Sytsma & Gottlieb, 1986).

Clarkia Pursh subsect. **Lautiflorae** Lewis & Lewis, Univ. Calif. Publ. Bot. 20: 319. 1955. TYPE: *Oenothera biloba* Durand, J. Acad. Nat. Sci. Philadelphia, Ser. 2, 3: 87. 1855. [≡ *Clarkia biloba* (Durand) Nelson & Macbride]

Petals 10–30 mm long, lavender to pink, not differentiated into bands or zones of different color; mature stigma usually held above the stamens, the stamens maturing first; immature capsule conspicuously 8-ribbed or grooved.

3. **Clarkia biloba** (Durand) Nelson & Macbride, Bot. Gaz. (Crawfordsville) 65: 60. 1918. *Oenothera biloba* Durand, J. Acad. Nat. Sci. Philadelphia, Ser. 2, 3: 87. 1855. *Godetia biloba* (Durand) Watson, Bot. Calif. 1: 231. 1876. *Oenothera prismatica* var. *biloba* Léveille, Monogr. Onothera 264. 1908. LECTOTYPE: grown from seed at Louisville, Kentucky, U.S.A., 1855, *Short s.n.* (P).

3a. **Clarkia biloba** subsp. **australis** Lewis & Lewis, Univ. Calif. Publ. Bot. 20: 322. 1955. TYPE: U.S.A. California: Mariposa Co., Hwy. 140, Merced River, 1 mi. W of junction with the South Fork of the Merced River, 18 June 1949, *Lewis & Lewis 628* (LA).

3b. **Clarkia biloba** subsp. **biloba**

3c. **Clarkia biloba** subsp. **brandegeae** (Jepson) Lewis & Lewis, Univ. Calif. Publ. Bot. 20: 323. 1955. *Godetia dudleyana* f. *brandegeae* Jepson, Univ. Calif. Publ. Bot. 2: 334. 1907. *Godetia dudleyana* var. *brandegeae* (Jepson) Jepson, Man. Fl. Pl. Calif. 675. 1925. TYPE: U.S.A. California: Eldorado Co., Simpson Ranch, Sweetwater Creek, 29 May 1907, *Brandegee s.n.* (UC).

4. Clarkia dudleyana (Abrams) Macbride, Contr. Gray Herb. 56: 54. 1918. *Godetia dudleyana* Abrams, Fl. Los Angeles 267. 1904. TYPE: U.S.A. California: Los Angeles Co., Little Santa Anita Canyon at 2,500 ft., s.d., *Abrams 2625* (DS).

Godetia bottae var. *usitata* Jepson, Univ. Calif. Publ. Bot. 2: 332. 1907. TYPE: U.S.A. California: San Bernardino Co., s.d., *Parish 3672* (holotype, UC; isotype, GH).

5. Clarkia lingulata Lewis & Lewis, Madroño 12: 35. 1953. TYPE: U.S.A. California: Mariposa Co., Merced River, 0.2 mi. W of bridge over South Fork of the Merced River, 8 June 1947, *Lewis & Lewis 334* (LA).

6. Clarkia modesta Jepson, Man. Fl. Pl. Calif. 673. 1925. *Godetia epilobioides* var. *modesta* (Jepson) Jepson, Fl. Calif. 2: 585. 1936. *Phaeostoma modesta* (Jepson) Heller, Leafl. W. Bot. 2: 221. 1940. TYPE: U.S.A. California: Fresno Co., Waltham Creek, San Carlos (Diablo) Range, s.d., *Jepson 2690* (JEPS).

Clarkia Pursh subsect. **Micranthae** Lewis & Lewis, Univ. Calif. Publ. Bot. 20: 330. 1955. TYPE: *Oenothera epilobioides* Nuttall ex Torrey & Gray, Fl. N. Amer. 1: 511. 1840. [≡ *Clarkia epilobioides* (Nutall ex Torrey & Gray) Nelson & Macbride]

Petals white, as much as 10 mm long, not flecked; mature stigma not held above the stamens; stigma and stamens maturing more or less simultaneously; anthers adhering to the stigma and depositing pollen directly upon it; immature capsule subterete, not conspicuously ribbed.

7. Clarkia epilobioides (Nuttall ex Torrey & Gray) Nelson & Macbride, Bot. Gaz. (Crawfordsville) 65: 60. 1918. *Oenothera epilobioides* Nuttall ex Torrey & Gray, Fl. N. Amer. 1: 511. 1840. *Sphaerostigma epilobioides* (Nuttall ex Torrey & Gray) Walpers, Repert. Bot. Syst. 2: 78. 1843. *Godetia epilobioides* (Nuttall ex Torrey & Gray) Watson, Bot. Calif. 1: 231. 1876. TYPE: U.S.A. California: San Diego, s.d., *Nuttall s.n.* (NY).

Clarkia Pursh subsect. **Prognatae** Lewis & Lewis, Univ. Calif. Publ. Bot. 20: 332. 1955. TYPE: *Clarkia similis* Lewis & Ernst, Madroño 12: 89. 1953.

Petals pale pink to nearly white, flecked with purple in the lower half, not differentiated into distinct zones of color, 6–12 mm long; anthers usually free, maturing with the stigma; stigma not held above the stamens.

8. Clarkia similis Lewis & Ernst, Madroño 12: 89. 1953. TYPE: U.S.A. California: San Diego Co., 7.6 mi. W of Ramona, 22 Apr. 1951, *Lewis, Lewis, Ernst & Mathias 773* (LA).

Clarkia Pursh subsect. **Sympherica** Holsinger & Lewis, subsect. nov. TYPE: *Clarkia lewisii* Raven & Parnell, Ann. Missouri Bot. Gard. 64: 642. 1977 [1978].

Petalis 10–35 mm longis, plerumque 15 mm longioribus, duobus vel tribus coloris zonae; staminibus plerumque quam stylo brevioribus; proterandrus; ovario plerumque 4-canaliculato.

Petals 10–35 mm long, usually more than 15 mm long, differentiated into two or three zones of color; mature stigma held above the stamens, the stamens maturing first; immature capsule usually 4-grooved.

9. Clarkia cylindrica (Jepson) Lewis & Lewis, Madroño 12: 33. 1953. *Godetia bottae* var. *cylindrica* Jepson, Univ. Calif. Publ. Bot. 2: 332. 1907. *Godetia cylindrica* (Jepson) Hitchcock, Bot. Gaz. (Crawfordsville) 89: 352. 1930. TYPE: U.S.A. California: Fresno Co., Waltham Creek, near Alcade, s.d., *Jepson 2656A* (JEPS).

9a. Clarkia cylindrica subsp. **clavicarpa** Davis, Brittonia 22: 283. 1970. TYPE: U.S.A. California: Tulare Co., Exeter to Springville road, 1.5 mi. E of the County Fire Station, 6 June 1947, *Lewis & Lewis 300* [holotype, LA (the specimen on the far right); isotypes, LA, RSA].

9b. Clarkia cylindrica subsp. **cylindrica**

10. Clarkia lewisii Raven & Parnell, Ann. Missouri Bot. Gard 64: 642. 1977 [1978]. TYPE: U.S.A. California: Monterey Co., Point Lobos, along the trail to China Cove from the end of the road, 26 June 1947, *Lewis & Lewis 498* (LA).

11. Clarkia rostrata Davis, Brittonia 22: 281. 1970. TYPE: U.S.A. California: Mariposa Co., Hell Hollow, Merced River Canyon, 3.3 mi.

N of Bear Valley on California Hwy. 49, 17 May 1968, *Lewis, Bloom & James 1424* (LA).

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HOLSTIANTHUS, A NEW GENUS OF RUBIACEAE FROM THE GUAYANA HIGHLAND

Up to the present time 11 genera of Rubiaceae are known to be endemic to the flora of the Guayana Highland. They include the following: *Cephalodendron*, *Maguireocharis*, and *Neblinathamnus* (Steyermark, 1964, 1972) from Cerro de la Neblina; *Aphanocarpus* Steyermark (1965) from sandstone table mountains and adjacent plateaus of Estado Bolívar; *Coryphothamnus* Steyermark (1965) from Auyan-tepui; *Duidania* Standley (1931) from the sandstone mountains of Duida, Huachamacari, and Marahuaca; *Chondrococcus* Steyermark (1972) [now known as *Coccochondra* Rauschert (1982)] from the Serranía Parú; *Maguireothamnus* Steyermark (1964) from various table mountains of the Venezuelan Guayana; *Merumea* Steyermark (1972) from Cerro Sipapo of the Venezuelan Guayana and the Merume Mountains of Guyana; *Pagameopsis* Steyermark (1965) from various tepuis of the Venezuelan Guayana and adjacent northern Brazil; and *Chalepophyllum* Hook. f. (1873a, 1873b) from southeastern Venezuelan Guayana and adjacent Guyana. Although such genera as *Gleasonia* Standley (1931), *Platycarpum* Humb. & Bonpl. (1809), *Sipaneopsis* Steyermark (1967), and *Dendrosipanea* Ducke (1935) show the greater part of their diversity within the Guayana Highland, they may also occur in lowland savannas, as in the case of *Sipaneopsis* and *Dendrosipanea*, or in Amazonian Colombia and Brazil.

Holstianthus Steyermark, gen. nov. TYPE: *H. barbigularis* Steyermark.

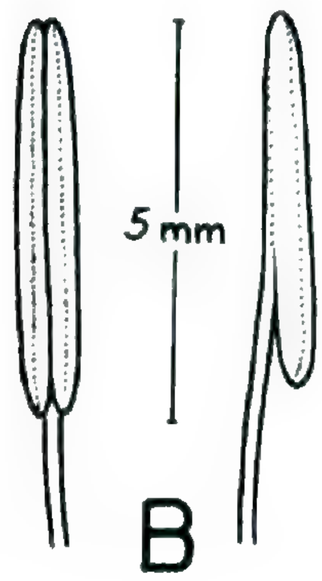
Inflorescentia 1–3-flora plerumque axillaris pedunculata basi bibracteata. Calycis lobi aliquantum inaequales persistentes. Corollae extus salmoneo-rubrae, lobis 5 in aestivatione contortis, tubi intus orificio dense barbato pilis luteis elongatis exsertis munito. Ovarium 2-loculare, ovulis numerosis in placenta axillari insidentibus. Fructus non dehiscens siccus osseus, seminibus numerosis exalatis aliquantum angulatis subcompressis, pagina minute cellulosa. Frutex. Stipulae interpetiolares persistentes basi subtriangulares in appendicem subulatam abrupte desinentes. Genus monotypicum.

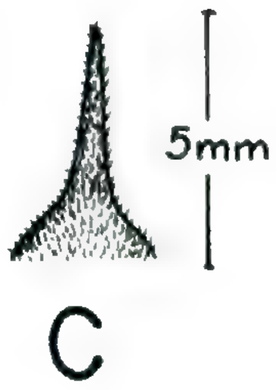
The genus is named for Bruce Holst, who collected the type material and served as botanical assistant on the expedition to Cerro Marahuaca.

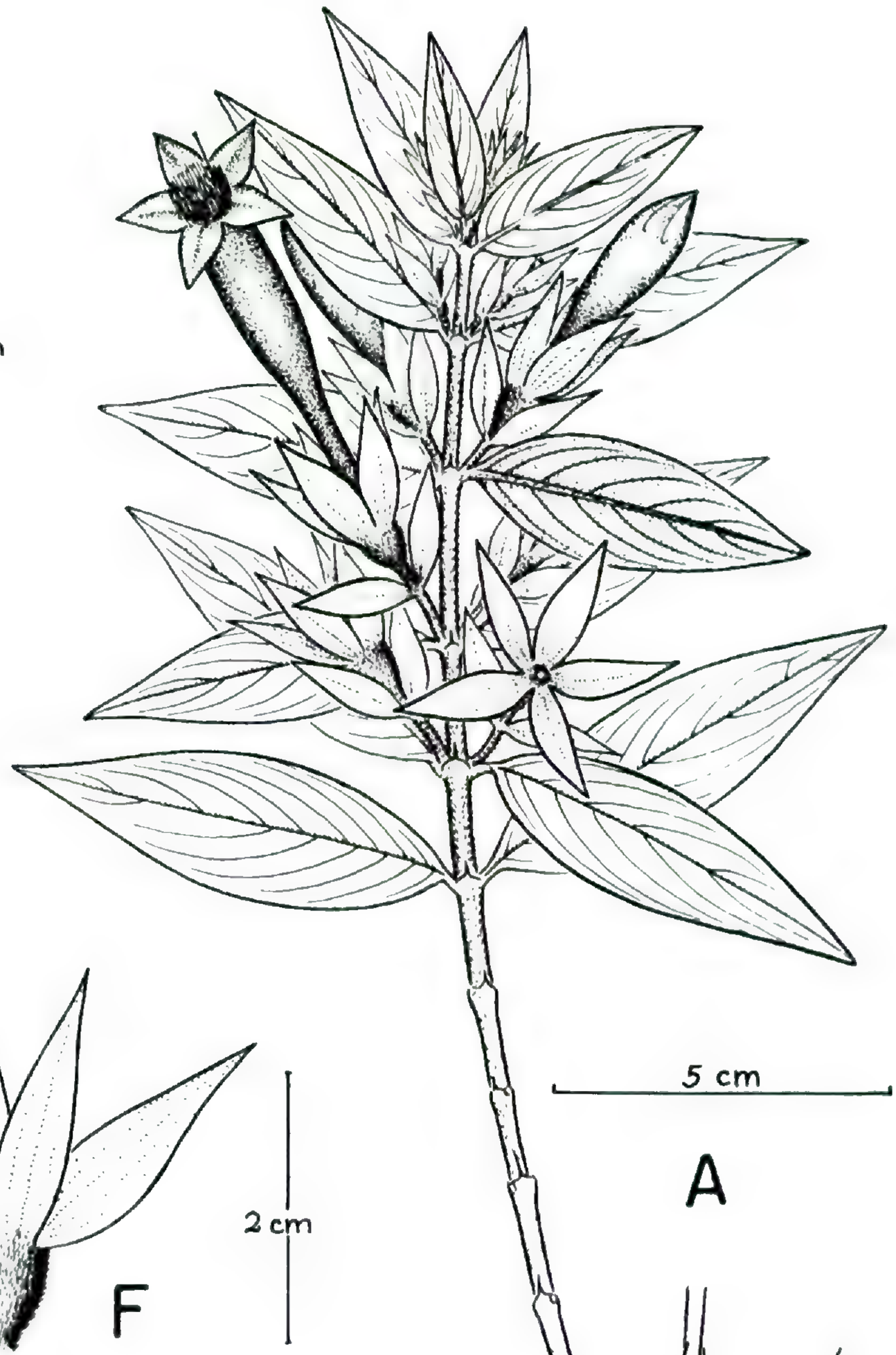
Holstianthus barbigularis Steyermark, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Atabapo, forested steep sandstone SE-facing slopes and bluffs, above branch of Caño Negro, Cerro Marahuaca, S-central portion, downstream from "Sima Camp," 3°43′N, 65°31′W, 1,220–1,350 m, 23–24 Feb. 1985, *Steyermark & Holst 130637* (holotype, MO; isotype, VEN). PARATYPE: same locality and date, *Steyermark & Holst 130664* (MO, VEN).

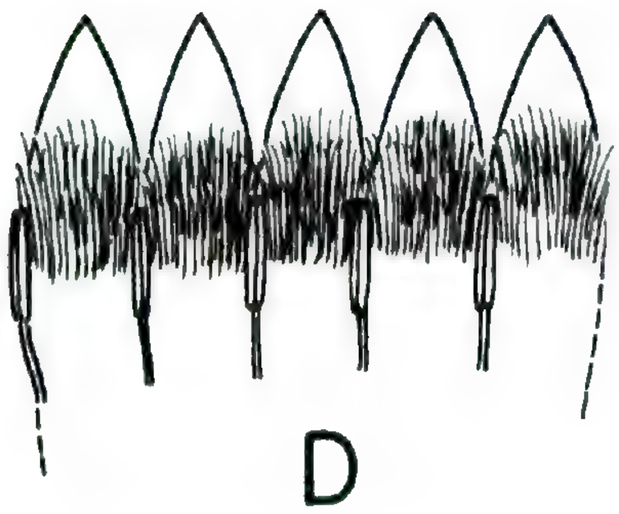
Frutex 0.6–2 metralis; foliis lanceolato-oblongis vel oblongo-ellipticis apice acutis vel acuminatis basi subacutis vel obtusis 4.5–11.5 cm longis 1.5–3.5 cm latis, subtus hirtellis; inflorescentia plerumque axillari, floribus pedicellatis, pedicellis 4–12 mm longis dense cano-tomentosis; bracteis sub pedicellis ovatis acutis vel acuminatis 8–18 mm longis 4–6 mm latis; bracteis sub pedunculo majoribus; calycis lobis 5 imbricatis, 3 exterioribus majoribus late lanceolatis vel ovato-lanceolatis acuminatus 2–2.5 cm longis 8–9 mm latis extus strigillosis intus glabris, 2 interioribus lanceolatis 2–2.5 cm longis 8–9 mm latis; corolla infundibuliformi 6.3 cm longa, extus glabra, tubo 2.3 cm longo 3.5–4 mm lato intus glabro, limbo intus orificio dense barbato aliter glabro, lobis ovato-lanceolatis acuminatis 10 mm longis 5 mm latis; staminibus 5 superne insertis, antheris 4.5–5 mm longis; fructu endocarpio tenui 0.2 mm crasso osseo mesocarpio 0.5 mm crasso instructo; seminibus oblongo-subellipticis 0.75–1.5 mm longis.

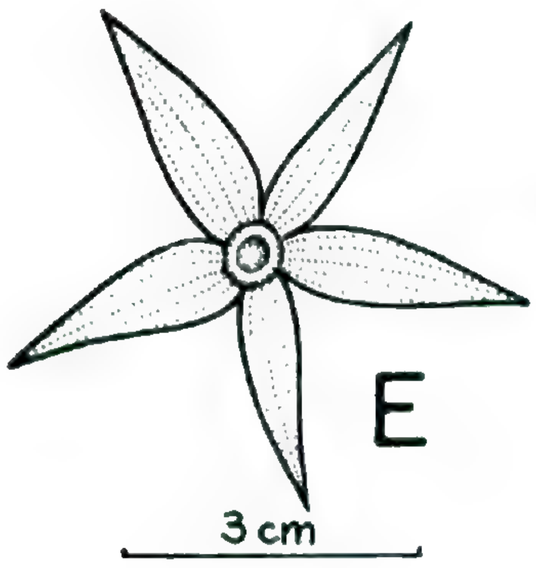
Shrub 0.6–2 m tall; young stems densely hirtellous. Stipular sheath subdeltoid, 1–3 mm long, 2–4 mm wide, densely strigillose-hirtellous without, abruptly terminating in a subulate, strigillose appendage 3–7 mm long, on sterile leafy shoots longer. Leaves subcoriaceous, lanceolate-oblong or oblong-elliptic, acute to acuminate at apex, subacute to obtuse at base, 4.5–11.5 cm long, 1.5–3.5 cm wide, glabrous above except strigose along midrib and on some lateral nerves; petioles 1–4 mm long or the uppermost leaves subsessile, densely strigillose. Inflorescence terminal or axillary, 1–3-flowered, 2-bracteate, pedunculate; peduncle divaricate, 7–14 mm long, the upper ones shorter, densely canescent. Bracts subtending each pedicel ovate, acute to acuminate, 8–18 mm long, 4–6 mm wide, glabrous above, sparsely hirtellous below, minutely ciliolate on margins; bracts subtending peduncle larger, 18–22 mm long, 8–10 mm wide. Calyx

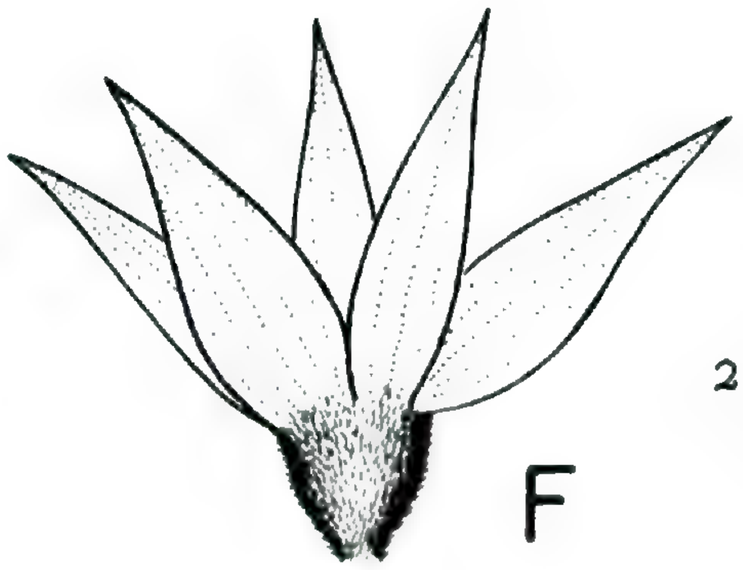


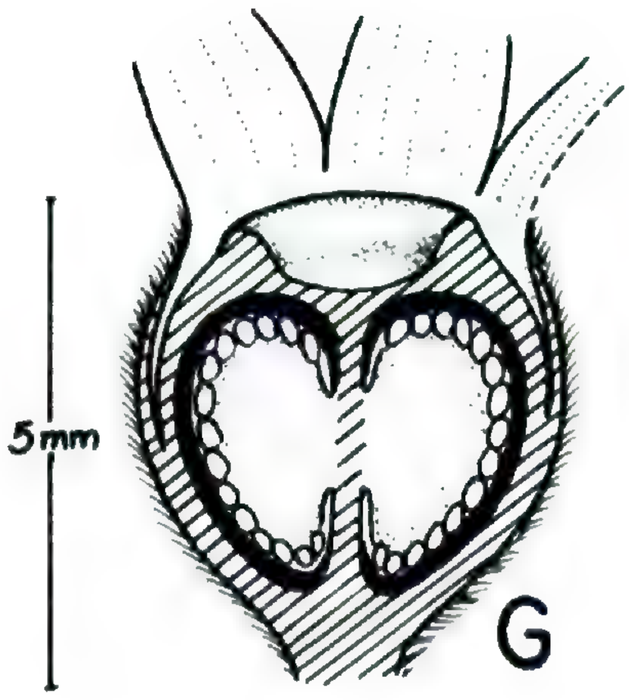


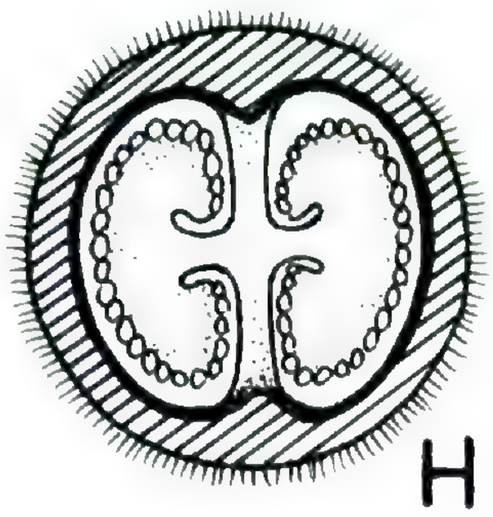












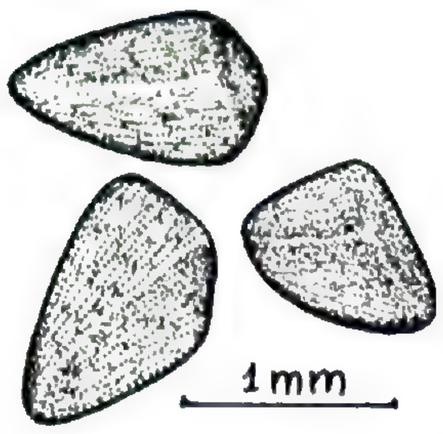


FIGURE 1. *Holstianthus barbigularis* Steyermark.—A. Habit.—B. Stamen, abaxial and lateral views.—C. Stipule.—D. Interior of upper portion of corolla limb and lobes.—E. Calyx lobes and disk, seen from above.—F. Calyx and hypanthium.—G. Vertical section through ovary.—H. Transverse section through ovary.—I. Seeds.

lobes 5, imbricate, persistent, somewhat unequal, 3 outer ones broadly lanceolate to ovate-lanceolate, acuminate, 2–2.5 cm long, 8–9 mm wide, finely longitudinally 5-nerved, moderately substrigillose without, glabrous within, 2 inner lobes lanceolate, 2–2.5 cm long, 8–9 mm wide. Hypanthium subcampanulate, 3–6 mm long, 5–7 mm wide, densely gray-hirtellous without. Corolla salmon-red, infundibuliform, 6.3 cm long, glabrous without, tube 2.3 cm long, 3.5–4 mm wide, expanded above into a limb 3 cm long, 10 mm wide at the summit, densely barbate within at the throat with elongate yellow hairs 8–10 mm long exserted beyond the orifice, lobes equal, ovate-lanceolate, acuminate, 10 mm long, 5 mm wide at the base. Stamens inserted in the upper part of the limb; anthers linear, dorsifixed, rounded at both ends, attaining summit of orifice but not exserted, 4.5–5 mm long, glabrous; filaments 3–4 mm long, glabrous, inserted 7–8 mm below orifice. Disk fleshy, annular, 5 mm across. Style filiform, 7–7.5 mm long, glabrous; stigma lobes 2, erect; ovary 2-celled; ovules numerous, arranged on all sides of a rounded thickened placenta, subelliptic-oblong; fruiting hypanthium 7–10 mm long, 7–8 mm wide. Fruit dry, osseous, indehiscent, the endocarp firm, thin, 0.2 mm thick; mesocarp 0.5 mm thick; seeds pale yellow-brown, somewhat angled and dorsiventrally subcompressed, subelliptic-oblong, 0.75–1.5 mm long.

The genus *Holstianthus* can be properly accommodated in the tribe *Rondeletieae* by virtue of its dry fruit, numerous, exalate or exappendiculate seeds, and contorted corolla lobes. Among most other genera of the tribe having contorted corolla lobes, it is at once separated by its indehiscent fruit. From *Sipaneopsis,* a member of the tribe with indehiscent fruit, *Holstianthus* differs in the contorted corolla lobes, numerous, subcompressed, subangulate seeds, densely barbate orifice of the corolla with elongated yellow hairs, subunequal, prominent calyx lobes, bibracteate pedicels, large, reddish infundibuliform corolla, and mainly axillary inflorescences.

The new genus herewith described was collected on a recent expedition to a previously unexplored sector of Cerro Marahuaca in Territorio Federal Amazonas. The trip was made possible through helicopter support provided by the Terramar Foundation of Caracas, Venezuela. Grateful appreciation is hereby given to Armando and Fabian Michelangeli of the Foundation for having furnished the logistics on this expedition.

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—Julian A. Steyermark, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

A NEW SPECIES OF *SOLANUM* (SOLANACEAE) FROM MADAGASCAR

Solanum mahoriensis D'Arcy & Rakotozafy, sp. nov. TYPE: Cultivated, Missouri Botanical Garden, *D'Arcy 15487a*. Seed from Madagascar. Antsiranana (Diego-Suarez): forest of Mahory, ca. 6 km S of Marataolana (ca. 12 km S of Anivorano Nord), 12°48′S, 49°14′E (holotype, MO; isotype, TAN, duplicates to be distributed).

Frutex ad 1 m altus, sparse pubescens pilis stellatis, spinis rectis nemio armatis. Folia lobata, armata, glabrata. Flores purpurei, staminibus angustis. Bacca viridis odorata, calyce accrescenti tecta.

Robust herb or shrub 1 m tall; branching from near the base, branches slender, arching, wand-like, to 1.5 m long, pubescent with occasional long-stalked often porrect, pauciradiate hairs that lack midpoints, copiously armed with acicular, sometimes flattened, straight, retrorse spines to 12 mm long, these often with a terminal stellate hair or with one or more hairs near the base. Leaves obovate, to 25 cm long, 16 cm wide, basally dimidiate, 1–3-pinnately lobed, with ca. 4 major lobes on each side, lobed three-fourths way to the midrib, on aged leaves lobed three-fourths way to the midrib, the sinuses rounded to slightly angular, the lobes apically obtuse or acute; major veins drying elevated and darker beneath, the costa and major lateral veins bearing numerous spines as those on the stem, the lamina glabrate above but with sparse short-stalked multangulate hairs beneath, the margin and veins with copious stellate hairs; petiole slender, 10–35 mm long, stellate pubescent and sparingly armed. Inflorescences short racemes inserted near top of internodes, the peduncle slender, 8 mm long, stellate-pubescent and with numerous small straight spines, the pedicels 8–10, ca. 7 mm long, resembling the peduncle but with smaller spines. Flowers heterostylous, calyx cupular, basally colored with copious short reddish brown, dark-based spines and reddish brown stellate hairs, whitish distally with stellate hairs, the tube cupular, 7–8 mm long (3–4 mm long in short-styled flowers), whitish mauve, the lobes subulate, 10 mm long (4 mm long in short-styled flowers), the apical one-half or one-third green; corolla mauve, darker at the center and drying with fainter tips, the lobes darker with the costa elevated and darker, the sinuses rounded to slightly angulate, the lobes ca. 10 mm long (8 mm long in short-styled flowers), glabrous within, stellate-pubescent outside except on the sinuses where puberulent with reduced simple trichomes; stamens 5, equal, the anthers yellow, subsessile, narrow, 8 mm long (4.5 mm in short-styled flowers), the terminal pores minute, the filaments purplish as the corolla, 0.5 mm long, glabrous; ovary white, ovoid, 2 mm long, the apical half glandular with minute, gland-tipped, simple hairs, the styles white, ca. 18 mm long, overtopping with stamens and apically recurved (those of the short-styled flowers rudimentary with stigmas not differentiated), with a few greatly reduced simple, gland-tipped hairs and occasional branched hairs on the basal portion, stigma subglobose, dark green. Fruit usually one per inflorescence, pendant, a perfumed globose berry, (2–)3 cm across, 2-locular, loosely enveloped by the accrescent bladder-like calyx, the calyx 4 cm across, 4 cm long, proximally sulcate at the major veins, whitish, copiously armed with acicular spines; pedicel 15 mm long, 2 mm thick; seeds numerous, stramineous, compressed, 4 mm long.

Solanum mahoriensis is a member of *Solanum* subg. *Leptostemonum* (Dun.) Bitt., which includes spiny species with slender anthers. Its probable sectional placement is unclear.

The heterostyly in this species resembles that well known in many other species of subg. *Leptostemonum*: the first flowers have long styles and bear fruit, the later short-styled flowers have greatly reduced ovaries and do not bear fruit. Anthers of both types of flower are polleniferous.

The spiny lobed leaves and inflated fruit-enveloping calyx of *Solanum mahoriensis* are strongly reminiscent of *Solanum sisymbriifolium* Lam. of South America, but that species has a white flower, a smaller, scarlet fruit, and a less spreading growth habit. The fruit of this species remains green, and it has a strong perfume-like scent, an unusual condition for berries in the Solanaceae. However, the cut surface of the juicy berry has a tomato-like odor. The fruiting calyx is truly echinoid—resembling nothing more than a spiny sea urchin—and when old, the dark reddish brown spines contrast with the nearly white calyx walls. To judge from a reduction in pu-

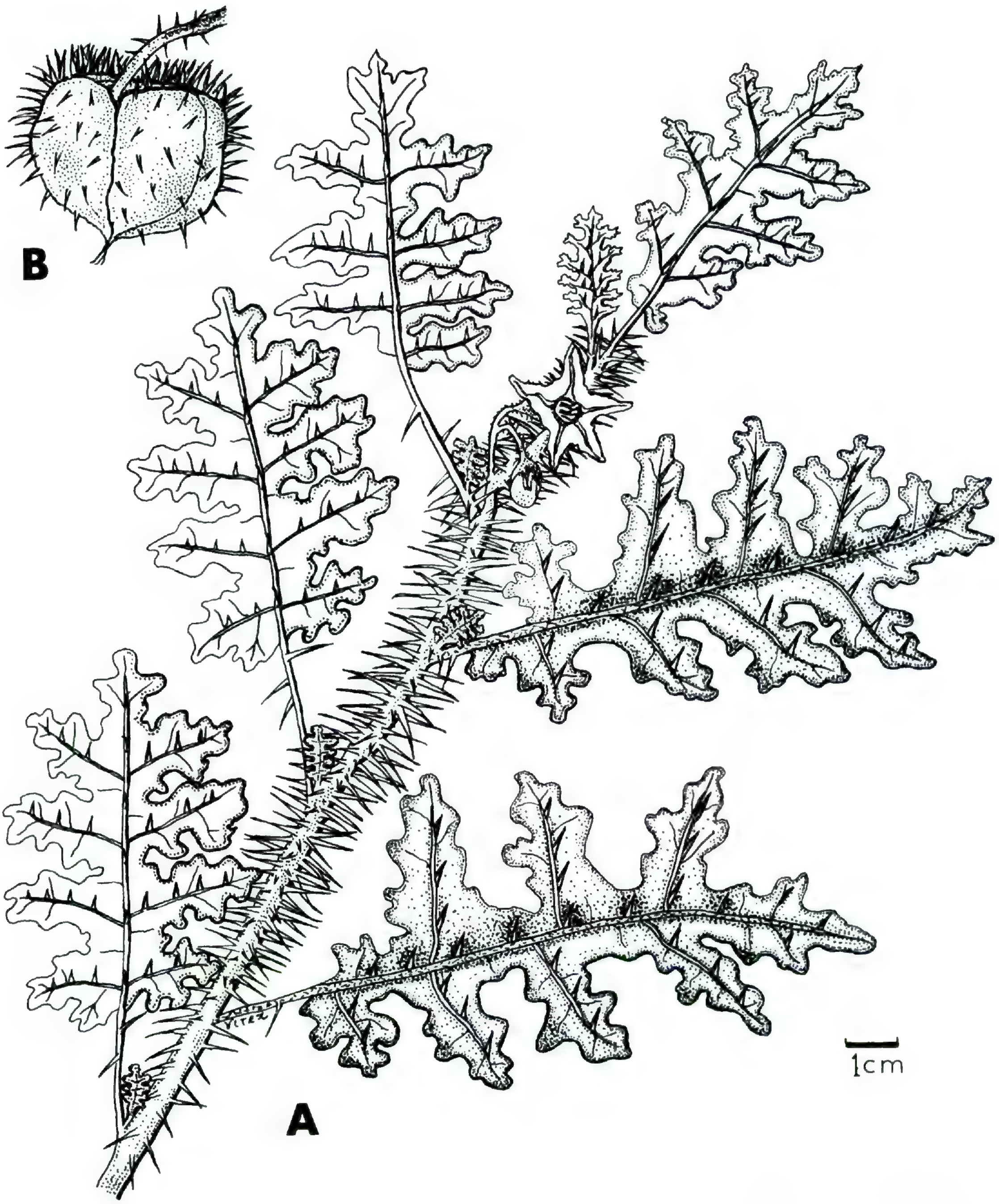

FIGURE 1. *Solanum mahoriensis* D'Arcy & Rakotozafy.—A. Habit.—B. Fruit. [After *D'Arcy 16045* (MO).]

bescence in the apical portion of the pedicel, the elongation of the pedicel in fruit may be confined to this apical region.

Solanum mahoriensis was found on level ground under a 60% canopy in the "Foret de Mahory," a wooded area ca. 6 km S of the village of Marataolana which is ca. 12 km S of Anivorano Nord. This locality (12°48′S, 49°14′E) is tropical, in the extreme north of the island, far from the temperate climates of southern Madagascar where the unusual endemic solanums of sect. *Croatii* D'Arcy occur.

Specimens examined. MADAGASCAR. ANTSIRANANA: vestige forestiére, sur basaltes, près de Marovato au N de l'Ankarana, 9/11/66, *Capuron 24561-SF* (MSF, P, TEF); forêt de Mahory, 6 km S of Marotaolana, ca. 12 km S of Anivorano Nord, *D'Arcy 15487* (MO, P, TAN); collines et plateaux calcaires de l'Ankarana, forêt tropophile, 300 m, *Humbert 18936* (MSF, P).

Supported by a grant from the National Geographic Society. Thanks are due also to Steve Kingsley, Antsiranana, who helped locate the species in the field.

—William G. D'Arcy, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63110; and Armand Rakotozafy, National de Recherches de Tsimbazaza, B.P. 4096, Antananarivo, Madagascar.

A NEW *PASPALUM* (POACEAE) FROM MESOAMERICA

The enormous pantropical and warm temperate genus *Paspalum* includes at least 400 species (Chase, 1929). *Paspalum* is recognized by the inflorescence of one or more unilateral racemes, the panicoid spikelets being plano-convex, often lacking lower glumes, and occurring solitary or in pairs on the lower side of the raceme rachis, with their upper glumes and fertile lemmas turned toward the center line of the rachis. The species described occurs on Cerro Uyuca, Honduras, an ancient volcanic peak near the town of El Zamorano. Because of its proximity to the Standley Herbarium of the Escuela Agricola Panamericana, Uyuca has been thoroughly botanized and is the type locality for a number of new species.

Paspalum uyucensis Pohl, sp. nov. TYPE: Honduras, 26 July 1951, *Freytag s.n.* Herbarium of G. B. Van Schaack 3274 (holotype, MO-3212543).

Gramen perenne caespitosum rhizomata curta, nodosa; vaginae infernae pilosae, superiores glabrae; nodi retrorsi-barbati; ligula truncata membranosa 0.5–0.8 mm longa; laminae planae, papilloso-pilosae, 8–15 cm × 8–11 mm; vagina ultima sine lamina. Inflorescentia terminalis, 6–9 cm alta; racemi 4–6, ascendentes, laxi; rhachis triquetra, ciliata, tenuis. Spiculae binatim, 1.4–1.5 mm longae, obovatae 1.5–1.7 : 1, brunneolae; gluma inferna carens; gluma superna triplo-nervata sparsim appressi-pilosa; lemma infernum (sterile), triplo-nervatum; lemma supernum (fertile) 1.5 mm longum, stramineum; palea striatula.

Caespitose perennial from short knotty rhizomes; basal scales papillose-pilose; culms 40–65 cm tall, erect, the bases swollen; internodes glabrous; nodes retrorsely bearded. Lower sheaths papillose-pilose, keeled; upper sheaths glabrous, the uppermost elongated, bladeless. Ligule a truncate membrane, 0.5–0.8 mm long; blades loosely papillose-pilose on one or both surfaces, 8–15 cm by 8–11 mm, flat, the midrib prominent beneath. Inflorescence terminal, 6–9 cm long, the peduncle slender, arcuate, exserted 5–12 cm; racemes 4–6, ascending or spreading, slender, 3–7 cm long; rachis triquetrous, ca. 0.3 mm wide, bearing scattered elongated hairs; pedicels usually somewhat united, the terminal one to 1 mm long. Spikelets paired, brownish purple, 1.4–1.5 mm long, obovate 1.5–1.7 : 1; lower glume absent; upper glume 3-nerved, sparsely appressed-pubescent, slightly shorter than the spikelet; lower lemma sterile, 3-nerved, glabrous; upper lemma fertile, 1.5 mm long, stramineous, elliptical 1.4 : 1; palea minutely striate; caryopsis elliptical 1.4 : 1, brownish.

Other specimens examined. HONDURAS. Cerro Uyuca, *Freytag s.n.*, Herb. Van Schaack 3273 (MO-2311478); Cerro Monserrat, *Castro 147 A* (MO-2926547).

This species is presently known only from upper pine and cloud forests on Cerro Uyuca and Cerro Monserrat in central Honduras at elevations of 1,400–2,000 m.

Paspalum uyucensis belongs to the informal group *Caespitosa* of Chase (1929). It is closest to *P. umbratile* Chase, from which it differs in its bearded nodes, more numerous racemes, smaller, broader spikelets, and 3-nerved glume and lower lemma.

Journal Paper Number J-12090 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa; Project 1833.

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CHASE, A. 1929. The North American species of *Paspalum*. Contr. U.S. Natl. Herb. 28: 1–310.

—Richard W. Pohl, Professor of Botany and Curator of the Herbarium, Department of Botany, Iowa State University, Ames, Iowa 50011.

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Contents continued from front cover

Phytochemical Aspects of Phylogeny in Hamamelidae *David L. Giannasi* 417

Phylogeny of the Hamamelidae: Taxonomic Index *David L. Dilcher & Daniel Macklin* ..... 43[illegible]

Phylogenetic Studies Using Protein Sequences within the Order Myrtales *P. G. Martin & J. M. Dowd* ..... 44[illegible]

Paleogene Phytogeography and Climatology of South America *Edgardo J. Romero* 449

New Taxa of *Caladium*, *Chlorospatha*, and *Xanthosoma* (Araceae: Colocasioideae) from Southern Central America and Northwestern Colombia *Michael H. Grayum* 462

New Taxa in *Oenothera* (Onagraceae) *Warren L. Wagner* 475

Studies in the Araliaceae of Nicaragua, and a New Widespread Species of *Oreopanax* *M. J. Cannon & J. F. M. Cannon* 481

NOTES

Chromosome Numbers of New Caledonian Plants *Gerald D. Carr & Gordon McPherson* ..... 48[illegible]

A New Combination in *Ludwigia* Sect. *Microcarpium* (Onagraceae) *Ching-I Peng* ..... 49[illegible]

Description of a New Section and Subsection in *Clarkia* (Onagraceae) *Kent E. Holsinger & Harlan Lewis* 491

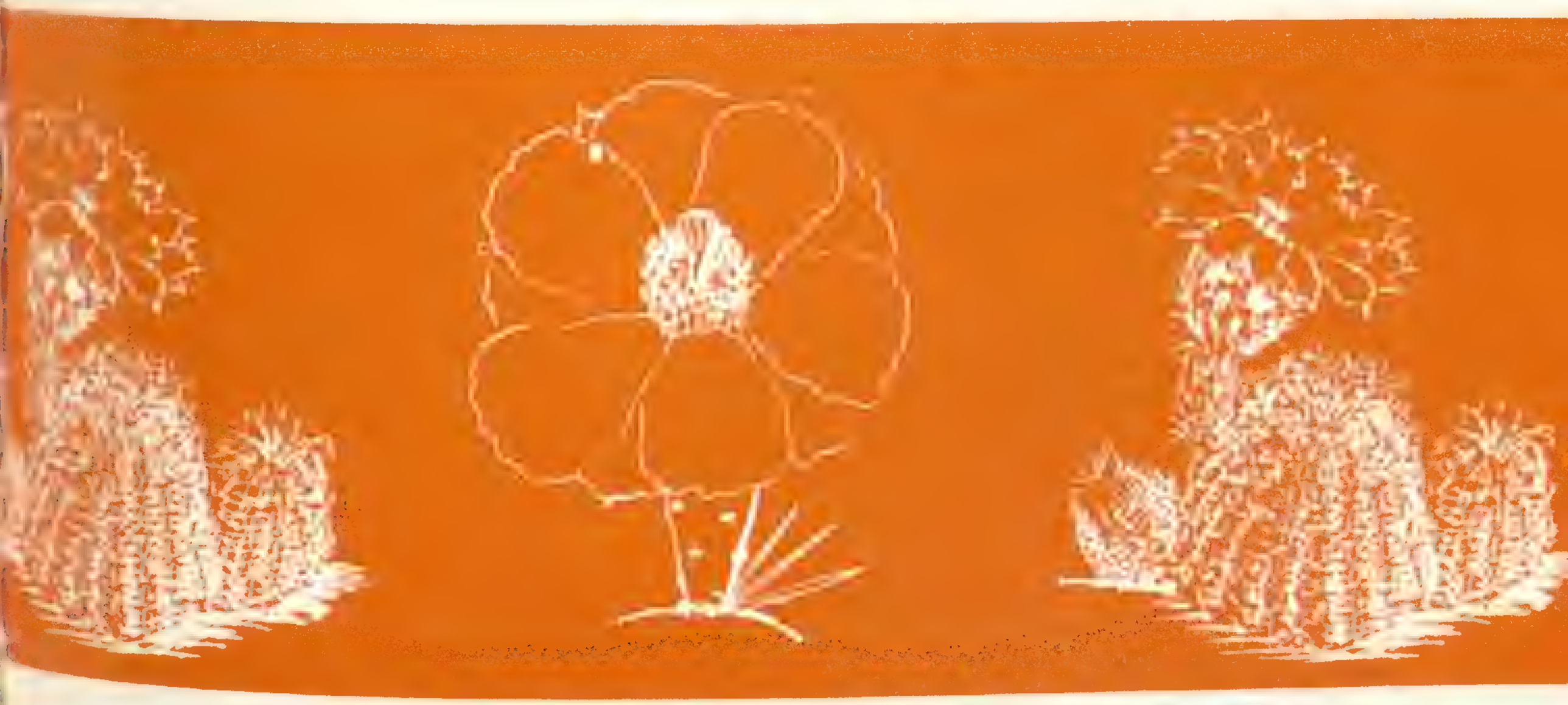
Holstianthus, a New Genus of Rubiaceae from the Guayana Highland *Julian A. Steyermark* 495

A New Species of *Solanum* (Solanaceae) from Madagascar *William G. D'Arcy & Armand Rakotozafy* 498

A New *Paspalum* (Poaceae) from Mesoamerica *Richard W. Pohl* 501

ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

VOLUME 73 1986 NUMBER 3



Sketches of cacti by G. Engelmann

CONTENTS

Topics in North American Botany. A Symposium Commemorating George Engelmann: The Thirty-First Annual Systematics Symposium *Marshall R. Crosby* 503

Instructions for the Collection and Preservation of Botanical Specimens *George Engelmann* 504

Changing Botany in North America: 1835–1860. The Role of George Engelmann *Elizabeth A. Shaw* 508

Augustus Fendler (1813–1883). Professional Plant Collector: Selected Correspondence with George Engelmann *Michael T. Stieber & Carla Lange* 520

The Ever-Changing Landscape of Cactus Systematics *Arthur C. Gibson, Kevin C. Spencer, Renu Bajaj, & Jerry L. McLaughlin* 532

Yuccas and Yucca Moths—A Historical Commentary *Herbert G. Baker* 556

Cenozoic History of Some Western American Pines *Daniel I. Axelrod* 565

A Historical Sketch of the Vegetation of the Mojave and Colorado Deserts of the American Southwest *Robert F. Thorne* 642

VOLUME 73
AUTUMN 1986
NUMBER 3

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TOPICS IN NORTH AMERICAN BOTANY, A SYMPOSIUM COMMEMORATING GEORGE ENGELMANN

The thirty-first annual Systematics Symposium of the Missouri Botanical Garden was held on 19 and 20 October 1984, the year that marked the centennial of the death of George Engelmann. Since George Engelmann was so important in the establishment of the basis of a scientific program at the Missouri Botanical Garden, and since he made so many early contributions to the knowledge of the flora of North America, we decided to commemorate him in the thirty-first annual Systematics Symposium. The papers presented at the Symposium are devoted to various aspects of botanical topics that interested Engelmann: *Yucca* and its pollination by moths; the pines; the family Cactaceae; aspects of the phytogeography and vegetation of the American West; and the interactions of Engelmann with his Harvard contemporary, Asa Gray. Certainly a one-day symposium could not hope to do full justice to a consideration of the contributions that Engelmann made to North American botany and the progress in the same areas in the century following his death, but the papers contained in this Symposium, when considered in connection with Engelmann's own publications and publications based on botanical specimens that he caused to be collected in the West, give an indication of the progress that has been made and the state of our knowledge in these areas.

Dr. Engelmann appeared at the closing session of the Symposium and presented a lecture, illuminated with slides, of his life and work.

This Symposium was supported in part by grant BSR-8311392, Gerrit Davidse, Principal Investigator, from the National Science Foundation to the Missouri Botanical Garden.

—Marshall R. Crosby, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

INSTRUCTIONS FOR THE COLLECTION AND PRESERVATION OF BOTANICAL SPECIMENS[1]

GEORGE ENGELMANN[2]

In gathering plants you will do well to pay attention to all the plants you come across, whether showy or unsightly. Do not neglect the latter on account of their appearance.

Collect if possible several specimens of the same plant, partly to show different states of the same species, and partly to be able to distribute them among different botanists.

Do not be deterred from gathering what appears to be the same species at different places and seasons. It may prove not to be the very same species, but only an allied species; or even if identical it is interesting for the study of geographical botany to have the same species from distant localities.

On the whole collect only such plants as you find in flower or fruit; but trees and shrubs ought to form an exception, as also smaller plants, if they afford some particular interest, either by their medicinal or other properties, great preponderance in certain districts, etc.

The most important part of the plant is the *flower* and *fruit*. Get if possible such specimens as present both states, flower and fruit, or both on different specimens. You will find plants which have fertile and sterile flowers distinct, they occur either on the same plant, as in the oaks, hickories, etc., or in different plants, as in the willows, cottonwoods and others. In both cases it is important to collect specimens which show each of them.

Many plants develope the leaves after the flowers, as the oaks, redbuds and many others. In these the flowers must be preserved, and later in the season, the leaves with the fruits; but great care must be taken to get them from the same species.

If the specimen you obtain is not too large, gather it entire, with the root or at least with part of it, so as to show the nature of that organ. Try to have the lower as well as upper leaves complete on the specimen, especially if they should differ from each other.

In case the specimen is too large for a sheet of paper, say more than 17 inches high, it may still be preserved entire, by bending or rather breaking (without entirely severing the parts) the stem in an acute angle. If necessary, this may be repeated and branches or leaves may also be treated in the same manner. This is better than cutting it in different segments, as these might become separated and much confusion ensue from this cause.

Of still larger plants, shrubs, trees, it is possible to take only a part, a branch, etc.; but if there should be different leaves on the plant, it will be necessary to cut off such leaves with a small piece of stem attached, and preserve them with the other specimens.

Make the specimen large enough to present a fair sample of the plant, its manner of growth, ramification etc.

It will be well to put your specimens in paper as soon as gathered; their parts are then fresh and still and are easily spread out in a neat way; but if they become flaccid they present much difficulty, and the dried specimens will appear unsightly.

Large specimens with thick stems or roots (bulbs especially) or even very clumsy flowers (as

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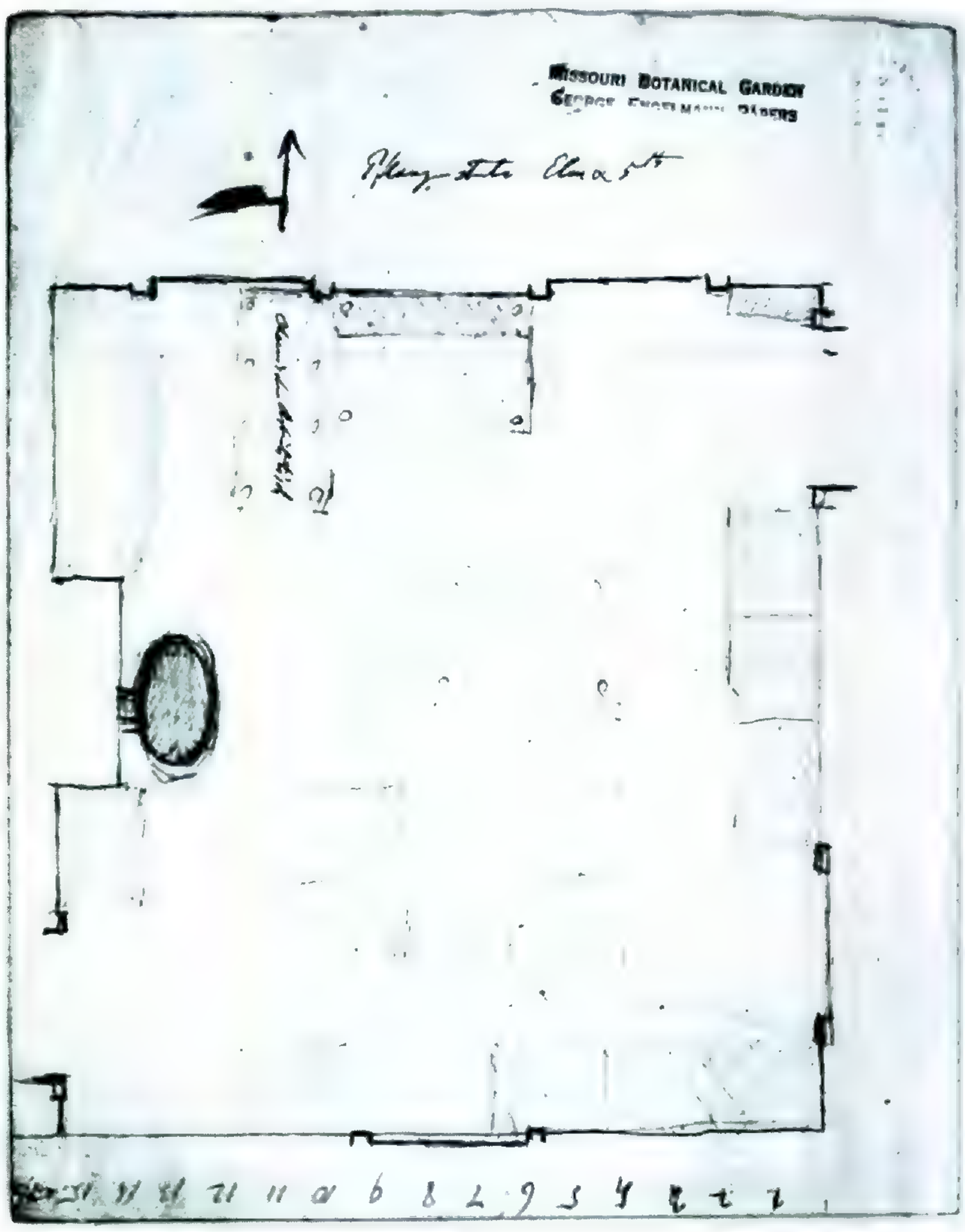
[1] These instructions exist as a manuscript in the George Engelmann Papers at the Library, Missouri Botanical Garden. They are printed here verbatim and unedited for spelling and punctuation. The manuscript is in a scrivener's hand, but there are a few corrections and additions by Engelmann, and he inserted an illustration of how to bend a specimen that is "too large for a sheet of paper."

Engelmann must have communicated these or similar instructions to those who collected for him. For example, Josiah Gregg wrote to Engelmann: "I could get no stiff pasteboard for portfolios" (10 February 1847); "I repeat that your instructions in every regard, have been of infinite use to me" (13 August 1847); "I have followed the system of numbering as you directed" (14 April 1849). (See, Diary & Letters of Josiah Gregg, M. G. Fulton, editor, 2 volumes, 1941, 1944, University of Oklahoma Press, Norman.) The Instructions provide a glimpse of plant collecting techniques in the middle of the last century and contain valuable pointers that the modern collector could take to heart. The legends to the illustrations were written on Dr. Engelmann's behalf by M. R. Crosby, who remains close to him through his correspondence and other papers.

[2] Address reprint requests to: George Engelmann, M.D., % M. R. Crosby, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166.

ANN. MISSOURI BOT. GARD. 73: 504–507. 1986.



An early St. Louis herbarium. After receiving my medical degree from Würzburg and spending a year studying in Paris, I came to the United States in 1832 on behalf of my family to investigate the possibilities of further investments in and emigration to Illinois and other western lands. I was naturalized in Philadelphia on December 24, 1832 and immediately proceeded to the Shiloh Valley of St. Clair County, Illinois. The next two years were unsatisfactory, though I made an interesting trip to the Arkansas Territory, losing my money, gun, and health along the way. Returning to Illinois, I decided to recross the River to St. Louis. Settling there in November 1835, I established my practice at 3rd and Chestnut Streets, planning only to remain long enough in this frontier town of 8,300 Anglo-Americans to save enough money to return to my native Germany. But, my practice flourished and the plants of the West were much more interesting than those of Europe. In 1847, against the advice of my friends, I moved to the far western part of town, to the southwest corner of 5th and Elm Streets, where Busch Memorial Stadium now stands. Here my medical practice continued to expand, and here I carried out many of my botanical investigations.

The sketch reproduced here is among my Papers, now preserved in the Library of the Missouri Botanical Garden, and shows my herbarium, which adjoined the medical office. As later workers have found, I used and reused paper (see Ann. Missouri Bot. Gard. 61: 907. 1974), and this sketch is on the back of later detailed drawings of *Isoëtes*. It is labelled "Pflanzstube Elm & 5th" at the top; the arrow points north. The up-side-down scale along the bottom is in English feet. The outline of the room indicates two windows on the north side and one each on the east and south sides of the room. Doors are located diagonally across from each other in the northeast and southwest corners. The dark oblong near the west wall is the free-standing, coal-burning stove, connected to a chimney by a short, dark pipe. There were two work tables, indicated with diagonal marks and circles in each corner as legs, one on the north wall, shelf above, and one near the center of the room. A third table, "Chemisch Arbeits Tisch," was placed perpendicular to the north wall, next to the work table with the shelf. The eight nearly square, cross-hatched structures along the east, south, and west walls are herbarium cases, as is the block of six, free standing, diagonally marked structures between the center table and the south wall. These cases' capacity was more or less equivalent to the steel ones in common use in the late twentieth century, so the room held about 14,000 specimens, when filled to capacity, a common problem even 150 years ago! There was a book shelf in the northeast corner, next to the door.

In 1869 I moved farther west yet, to Locust and Garrison Streets, and of course the herbarium went with me. I willed my herbarium to my only child, George Julius Engelmann, also a physician, but not a botanist. At that time the collection numbered about 98,000 specimens, including many nonvascular cryptogams. George J. donated the Herbarium to the Missouri Botanical Garden before 1890.

large thistle heads) often require to be split lengthways, so as to make them less bulky and injurious to the other plants in the herbarium.

Large fruits may be also split, or they may be preserved separately, wrapt in paper.

In putting up the specimens, spread them out in such a manner that all the different parts are seen, and the flowers, or some of the flowers, are laid open. If, however, time should be wanting, the plant may be laid in the paper just as it is.

The object of pressing plants, being to keep all the parts spread out smooth, and free from shrinking and wrinkling, but not to crush the more delicate organs, the flowers especially: the pressure should be moderate, say from 25 to 40 or at most 50 pounds in weight, so as to compress not destroy the organs, that they may afterward be examined. In traveling, two boards tightly strapped together will be quite sufficient to press plants. At home any weight of 30 or 40 pounds will do the same service.

After the specimen has been put in paper and pressed a while, it becomes necessary to change the layers of paper as soon as they have become damp from the moisture absorbed from the plant and to substitute dry ones for them. This ought to be repeated daily till the specimen is completely dried.

The most convenient method is to put the specimen in finer paper, say printing paper, then a layer of 2, 4 or 6 sheets of coarser bibulous paper, then a finer sheet with a plant and so forth. In changing the plants dry layers are substituted for the moist ones without removing the specimen from the finer sheet immediately touching it, which would be a tedious job, often injuring the specimen. The damp layers are then hung up or spread out and dried. The dried specimens are put aside between single leaves or sheets of paper, as many in one sheet as may be put there without injuring each other. When you have got a sufficiently sized bundle together, pack it either in a box of convenient size or in a fresh skin of some animal (hair inside) which will harden and shrink and form an easily handled and safe package.

A specimen is of much less value if not properly labeled. Therefore as soon as collected or when put up, attach a piece of paper to it, (the most simple method is to stick the stem through a hole in the paper,) on which you note at least *date* and *locality*; but if possible also every thing you can ascertain about the plant and which does not appear in the dried specimen itself: colour of flower, taste, smell, time of opening and closing of flowers, size of the plant, height, diameter of stem (in trees); nature of the soil (swamp, sand, rocks, open places, shade, etc.), whether frequent or rare. In parasitic plants it should be stated on which plant they grow. Besides this it will be well to number your plants as you collect them. This number will stand for a name and can always be referred to, especially if you keep a journal or some other memoranda of your collections, or in correspondence with other botanists, to whom specimens may be communicated.

You will further materially advance our knowledge of the vegetable kingdom, if you could collect any parts of plants or products of plants, which may be valuable or curious, such as medicinal roots, barks, gums, etc.

Make it an especial object to collect the fruits of plants which cannot be preserved in the herbarium, such as pine cones, nuts and others. Get also specimens of the woods. Of stems not thicker than 3 inches in diameter, take a whole piece 12 inches long, of larger ones only a section of the stem, showing bark, alburnum (exterior soft wood) and hard interior wood.

All such specimens of fruits, woods, roots, may very conveniently be labeled and marked with the same numbers as the specimens of the plant from which they are derived.

Collect also ripe seeds as many as you can get. Preserve them in their pods or fruits as they keep longer fresh in them. In wrapping them up, put if possible, a few leaves, a small branch, flowers or whatever part you can get, with them, and number them with the same number as the dried specimen of the same plant.

Seeds ought to be sent as soon as possible, as many lose their power to germinate if too old. They ought to be packed dry but not too tight as they may suffocate and moulder.

I have more especially studied several families to which I wish to direct your particular attention. I mention the *Asclepiadeae* and *Euphorbiaceae*, both comprising plants with milky juice, the first mostly with showy, umbellated flowers and silky appendage to the numerous seeds, the other with very inconspicuous greenish flowers and seeds. Further the *Pines*—then all the *parasites* such as the *Cuscutas* (Dodder or Lovevine) and the species of *Viscum* which grow on trees (Mistletoe) some of them of great interest on *Pines* in the Pacific region.

Above all others I mention the *Cactus* tribe, which I have not only studied (Fig. 1), but also cultivated. Specimens of Cacti in flower and in

fruit are important as well as entire plants, especially living ones for cultivation. For the herbarium the flower must be preserved with a piece of the plant attached to it, which shows the ridges or tubercles and spines. In your labels do not forget to describe the shape of the entire plant, number of ribs, number, shape, direction and color of spines in each bunch.

The Cacti are easily propagated by seed, but also living plants may be kept very long (from 6 to 12 months); they must be kept dry and not packed too close, nor before they have been kept for some time withering, or they will rot. Young plants are preserved better than old ones in this manner.

The most convenient apparatus for drying plants I have found in traveling is the following. Stitch or paste 2 or 3 sheets of coarse soft brown paper together at their backs, and string about 20 or 25 of such layers on one string, each fastened about one inch from the next. Put them in a strong pasteboard portfolio, and put several of these portfolios in a press of two pieces of plank, strapped together tightly. The strings of layers, when damp, are hung up in the open air and quickly dried, and put together again without loss of time. Finis.

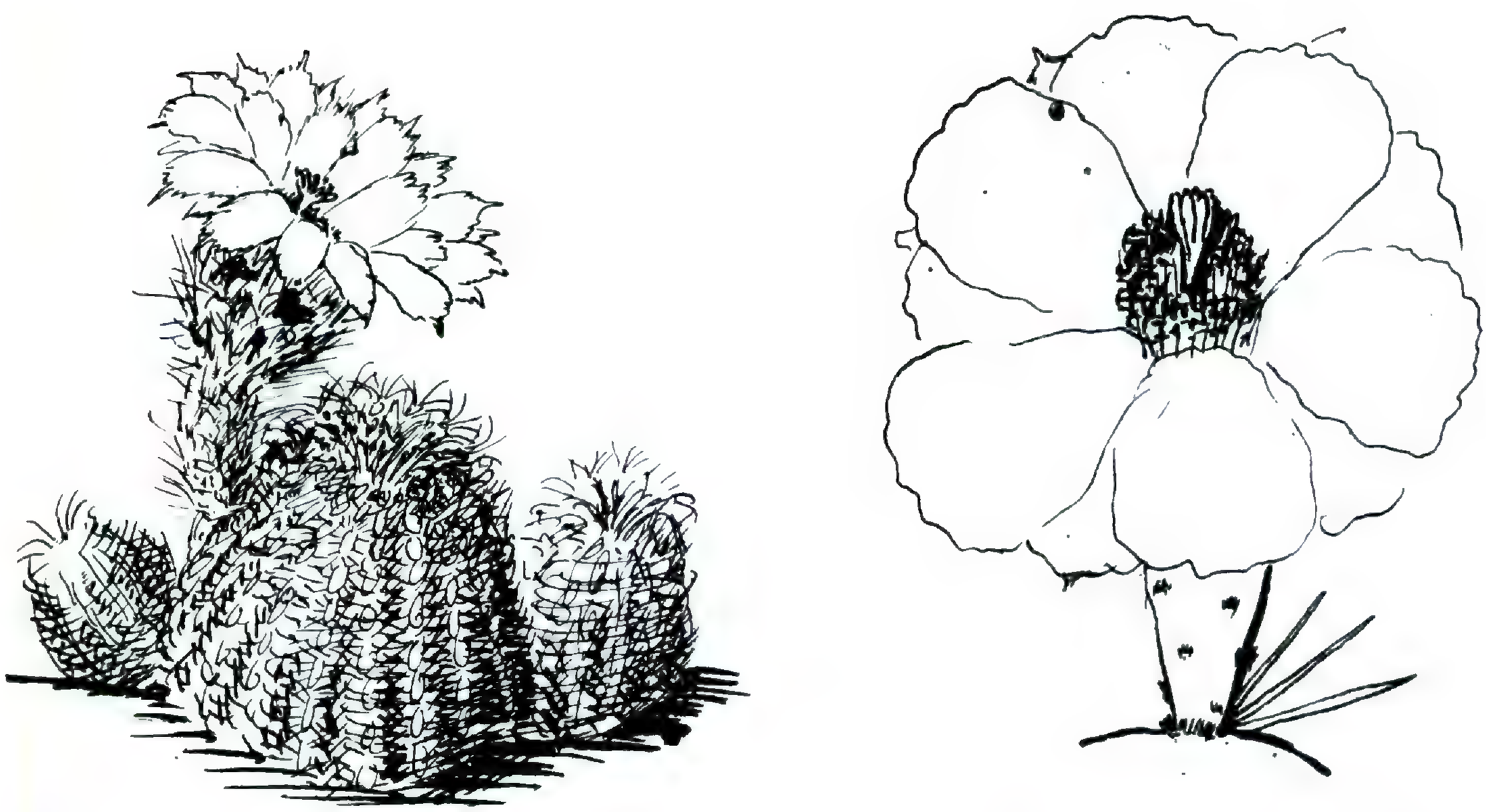


FIGURE 1. My botanical works were often beautifully illustrated, especially by Paulus Roetter, rather than by my own drawings. But, I made thousands of sketches of the plants I studied, and these are now in my Papers at the Missouri Botanical Garden. The western collectors who sent me material were especially good about supplying material of my groups. The two cacti reproduced here accompany four pages of notes I made from living material in 1845. These notes relate to my paper published with Dr. Gray, "Plantae Lindheimerianae, an enumeration of the plants collected in Texas, and distributed to subscribers," Boston J. Nat. Hist. 5: 210–264. 1845. I labelled the figure at the left *Cereus caespitosus,* now known as *Echinocereus reichenbachii* according to Benson's recent monograph. That at the right I called *Opuntia vulgaris*—a difficult complex: it may represent any one of a number of species of *Opuntia.*

CHANGING BOTANY IN NORTH AMERICA: 1835–1860 THE ROLE OF GEORGE ENGELMANN[1]

ELIZABETH A. SHAW[2]

Although the history of a subject or of a time should treat the parts played both by the "great"—or by the well-known—and by lesser figures, it is generally true that there are some few persons who stand out amongst the others and who give definition to the subject and time.

Even the most cursory look at botany in North America during the nineteenth century shows preeminent the triumvirate—Asa Gray, John Torrey, and George Engelmann. There were other outstanding botanists at the middle of the century—one might mention W. S. Sullivant and Edward Tuckerman—but it was Gray, Torrey, and Engelmann who had the greatest effect upon their adopted field. Their combined careers as botanists cover nearly seventy years. During this time, botany in North America developed from the simple collecting of plants and amassing of data with consequent assignment of genera and species into Linnaean pigeonholes, into something like modern botany.

I think, too, that examination of events in any field of science cannot be usefully done unless seen against the background of contemporary political, social, and intellectual realities. It can be done neither for the present nor for what might seem to have been a simpler and less complicated time. In any case, developments in botany in the United States during the middle of the nineteenth century were pulled along by the political events, and I have chosen to consider this time by looking at the relationship of botany to exploration in the American west and at the part played by one man, who was in the proverbial "right place at the right time."

The subject is botany on the American frontier and for the first sixty years of the century, which is nearly equivalent to the whole of American botany. Each of the three had a well-defined role.

Each was originally trained as a physician, but only Engelmann maintained a medical practice. Torrey, the oldest of the three, earned his living by teaching chemistry—at West Point, at Princeton, and at the College of Physicians and Surgeons in New York. Although Torrey had close ties with many correspondents in Europe, he was, *par excellence,* a botanist for North America. He was from the 1820s involved with preparing the botanical reports for government-sponsored expeditions and until after the Civil War plants from such expeditions went to Torrey, who had the overall responsibility for them. He prepared, for example, the final report on the botanical collections made by the Boundary Commission, which operated after the Mexican War. Torrey was much less concerned than were Gray and Engelmann in direct dealings with the private collectors active during the 1840s, but for many years it was he who would have the most direct connection with any official in Washington who might be helpful to botany.

Gray I see as the organizer among the three. From his arrival at Harvard in 1842, he was at the center of botanical activities in the United States and he came to have the greatest breadth of interests. His first trip abroad in 1838–1839 allowed him to make contacts and to open channels of communication that made Gray the internationalist among American scientists—certainly among botanists. For thirty years Gray provided a one-man abstracting service—presenting in the American Journal of Science and Arts, "Silliman's Journal," information about botanical work in Europe—news and reviews and criticism of work current.

Engelmann was the active physician with a busy and demanding practice in St. Louis and would seem to have had the least time free for botany. Engelmann would later prepare finely done treatments of several very difficult groups of plants, but during the 1840s *he* was the man at the frontier. Engelmann had the most direct

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[1] I am grateful to those people who heard, at greater length than they might have wished, about "Changing Botany in North America"; and I owe particular thanks to Bernice Schubert and to Peter Stevens for criticism and suggestions. Any eccentricities of interpretation are, of course, my own. I thank the Directors of the Harvard University Herbaria and of the Missouri Botanical Garden for permission to quote from manuscript materials in their care.

[2] The Gray Herbarium of Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

contact with collectors, both those operating privately and those in government employment or under government sponsorship; he gave advice and provided money, often his own, to men who might bring back plants. To him, the frontier was immediately at hand; writing in 1845 to Torrey [the letter quoted in Rodgers (1942)], Engelmann said, "You can have no idea how near we here consider ourselves now to Oregon & California; we mentally travel with those thousands of emigrants, and begin to think the Rocky Mts not much further off than the Alleghanies." And Engelmann could interpret the frontier to the colleagues back east, neither of whom would ever have any direct experience of the west in its frontier stage.

It has been suggested by the historian William Goetzmann (1966) in the introduction to "Exploration and Empire" that: "Exploration can be seen unfolding through major periods each characterized by a dominant set of objectives, particular forms of exploring activity, distinctive types of explorers, and appropriate institutions which governed these other factors."

The first of Goetzmann's periods runs from the expedition of Lewis and Clark (1804–1805) to about 1845; the second, from then to the start of the Civil War in 1861. The third is the time of the great multi-purpose, government-organized surveys after the War; King's Geological and Geographical Exploration of the Fortieth Parallel; Wheeler's Geographical Surveys of the Territories of the United States West of the 100th Meridian; Hayden's United States Geological Survey of the Territories; and Powell's exploration of the Colorado, which opened up the last bit of unknown territory in the continental United States. The "great surveys" were done by the end of the 1870s and exploration in the west was effectively complete. Ten years later the Report for 1890 of the Bureau of the Census declared that the continuous frontier was no more.

It seems, though, that so far as exploration that contributed to botany is concerned, it is more useful to think about four phases. For convenience I shall refer to "botanical exploration," with the understanding that we are dealing with exploration, for whatever proximate purpose, that brought back plants. The first period I shall recognize is Jeffersonian in conception and extends from the end of the Revolution to 1835; and it is not by chance that I've chosen to end this period the year in which George Engelmann settled in St. Louis to start his medical practice.

Although "manifest destiny" as a national slogan dates only from the 1840s, the idea that our national destiny lay in expansion westward to the Pacific, no matter that territories claimed by France, by Spain, and by England lay in the way, goes back at least to the beginning of the nation. For Thomas Jefferson, who combined great national pride with a passionate interest in natural history, the west was an area bound, someday, to become part of the United States, and during his presidency exploration west of the Mississippi was begun.

The second phase is, if the analogy be extended, Grayian in conception and continues from the 1830s through the end in 1848 of the Mexican War and includes the post-Mexican War boundary surveys; these were significant both for their scientific results and for bringing into the field the first concentration of botanical collectors—Charles Wright, John Bigelow, George Thurber, Arthur Schott, and Charles Christopher Parry—each man having other duties, but collecting plants as well.

The third period covers the years of the Pacific railroad surveys, which during the 1850s tied the newly acquired territory to the old United States; this period, for several reasons, ends at the end of the decade. The last phase is Goetzmann's period of "Great Surveys," up to the start of the twentieth century.

The two middle periods, 1835 to 1860, provide the background for the major changes in American botany and for the changes in the way in which exploration was carried out. It is exactly during this time that Engelmann was botanical gatekeeper, advisor, banker, and holder-of-hands for collectors setting out from St. Louis, or acting under his direction. But by the end of the 1850s the direction of Engelmann's botanical activities had changed; he had met Henry Shaw and in 1856 left St. Louis to spend more than a year in Europe visiting herbaria and buying specimens and books for Shaw's botanical garden. And the end of the 1850s marked the end of one phase of western exploration.

I think that a strong case can be made for recognition of 1860 as the time of a major shift in scientific activities in this country, and specifically, in botany. It is the historical divide between botany that was a continuation of a tradition eighteenth century in origin and botany that shows clearly the first signs of growth into its modern form.

There were several forces operating to change

botany in the United States. For twenty years the slow movement of science into the hands of professionals, i.e., people whose livelihood was gained from science, had been going on. The botanist as professional in this country can be dated from the appointment of Gray in 1842 to Harvard. But the event that had the most immediate effect upon botany was the passage by Congress of the Morrill Act of 1862, which founded the system of land-grant colleges that were required to specialize in "agricultural and mechanic arts." These colleges arose quickly after the Civil War, and following the requirement for agricultural arts, gave in their curricula a prominent place to botany. So, a crop of young botanists appeared, who were aware of, and eager to learn and use, new techniques from Europe. Indeed, some of them went to Europe for study and to acquire the degree of doctor of philosophy not then given in this country. When they returned, there were opportunities for them in the new universities, which, in contrast to the older ones, were unencumbered by the inertia of programs already established and sometimes a bit old-fashioned (Pauly, 1984). Quite suddenly botany diversified from collecting and taxonomy into a peacock's tail of possibilities.

The nature of exploration changed, too. During the Civil War little was done except in California, but then came the four great surveys. Although two, King's exploration of the fortieth parallel and Wheeler's surveys west of the 100th meridian, were under army sponsorship, they were civilian-organized and their goal was not mere military reconnaissance but the organized acquisition of scientific information. The parties were accompanied by men who were along, not to be an "assistant computer" as was Charles Wright, or a surgeon/naturalist, as was John Bigelow, but to be scientists. And one should add to this the changes brought by the increase in population, the appearance of foci of settlement in the west—Salt Lake City was founded in 1847 and Denver in 1858—and by railroads. People interested in plants were, more and more, in situ and travel was becoming easier and safer.

THE BOTANICAL FRONTIER IN 1835: PHYSICAL AND INTELLECTUAL

It is tempting to offer up the west of 1835 as a *tabula rasa* upon which its botanical story would be written during the next twenty-five years, but this would be quite wrong.

People's views of the west have been varied; it could be a place to live, a place to exploit, and a place to explore; and this last in two senses, the adventurer's desire to see what lay over the next hill, and the scientist's desire to have in his hands and under the microscope whatever lay over the next hill. The west initially offered seemingly unlimited opportunities for exploration, and for Thomas Jefferson it was a rich mine to disprove the claims then current and popular in Europe that America was a rude and miserable wasteland, degenerate and monstrous, noteworthy only for the poor quality of everything placed here by the creator (see, for example, de Pauw, 1768–1769).

After some unsuccessful attempts to get explorers into and across the west, Jefferson, as President, was able in 1804 to send Merriwether Lewis and William Clark up the Missouri and eventually to the mouth of the Columbia River, and they would bring back the first American-made collections of natural history materials. The plants were not the first from the west—in 1786 Jean-Nicolas Collignon with La Pérouse's expedition had sent back to France seeds of *Abronia umbellata* collected in California. Collignon and his shipmates died in the Solomon Islands, but the *Abronia* flowered in the Jardin des Plantes and was described as a new genus by de Jussieu. And still before 1800 Taddeus Haenke with the Malaspina expedition and Archibald Menzies with Vancouver's expedition had visited the west coast (McKelvey, 1955).

The greatest contributions to the botany of the west were made by Thomas Nuttall, of whom Gray said, ". . . no botanist has visited so large a portion of the United States, or made such an amount of observations in the field and forest. Probably few naturalists have ever excelled him in aptitude for such observations, in quickness of eye, tact in discrimination, and tenacity of memory" (Gray, 1844).

Nuttall as a young man emigrated from Yorkshire to Philadelphia in 1807 or 1808, and over the next twenty-five years wandered across the United States as it then was, and far beyond, protected, it seems, by innocence and a blazing and consuming interest in plants. He made three trips into the west. In 1810 Benjamin Barton of Philadelphia enlisted Nuttall to go to the Great Lakes, then northwest to Winnipeg, and return by the Missouri and Mississippi. Nuttall traveled during 1810 and 1811, part of the time with another Englishman, John Bradbury, whom he

had met in St. Louis, and got as far as Fort Mandan, North Dakota.

The second trip in 1818 and 1819 took Nuttall down the Ohio and up the Arkansas into eastern Oklahoma. In 1822 Nuttall was appointed curator of the botanical garden at Harvard, but after eleven years resigned to join an expedition headed up the Missouri and on to the Columbia. On this trip Nuttall again passed through St. Louis, but Engelmann was not yet settled there. Once on the west coast Nuttall made two trips to Hawaii and became the first "American" to collect in California, returning in 1836 to the east. This was his last trip; in 1842 Nuttall returned to England to take up a bequest that required him to spend most of his time at home (Graustein, 1967).

Indeed, by 1835 a map of areas from which plants were known would point—and this list is far from inclusive—to the following botanically-productive forays.

In 1819 and 1820 Stephen Long's "Yellowstone Expedition," with William Baldwin (who died en route) and then Edwin James, as botanist, did not get to the Yellowstone, but did make a great loop up the Missouri and North Platte rivers into eastern Colorado, and back to Missouri through the Texas panhandle, Oklahoma, and Arkansas. During the 1820s there was also botanical activity on the California coast, visited in 1826/1827 by Collie and Lay with Beechey's expedition; and in the northwest John Scouler and David Douglas (of the fir) collected in Washington and Oregon. By the end of the 1820s Jean Louis Berlandier was working in eastern and southern Texas (see McKelvey, 1955).

A bit later (1830–1832) Douglas was in California, as were Thomas Coulter and Nuttall, while another Thomas, Drummond, was collecting in east Texas. The northwest, still under British control, was visited by English collectors. To the south, plants were being collected in Oklahoma and Arkansas by two army surgeons, Zina Pitcher and Melines Leavenworth. During the 1820s a new kind of visitor to the west appeared—the European explorer, Humboldtean and romantic. The botanist among these was Prince Maximilian zu Weid-Neuweid, who during 1833 traveled up the Missouri to Fort McKenzie in Montana. Maximilian is best known as an ethnographer, and his trip is better known for the beautiful watercolors done by Karl Bodmer, but Maximilian did collect plants that were written up by Nees ab Esenbeck.

So the map shows that by 1835 we knew something of plants of the upper Missouri, of the northwest, of coastal California, and of parts of Texas, Oklahoma, and Arkansas. What the map shows *untouched* is more significant—the great unknowns of the Great Basin and the southern Rockies and of the lands to east and west—from San Antonio westward to San Diego; and the desire to fill in this blank would drive Asa Gray, and through him, American botany for the next fifteen years.

In 1835 anyone who wished to do serious work on American plants would have had to go to England, where so much of the material from the northwest and from California was, and to Geneva where de Candolle was working on the "Prodromus." North American botany was not well-known; but neither was it unknown, for there were several floristic works, some "national" in scope, others regional or local in coverage.

The first "national" flora was André Michaux' "Flora Boreali-Americana" published in France in 1803. Michaux had himself seen much of the United States; he and his son, François André, had traveled and collected in the southeast; and Michaux had made a remarkable trip north to Lake Mistassini in Quebec, at the latitude of the southern end of James Bay. The next was "Flora America septentrionalis" (1814), published in London by Ferdinand Pursh, pirate and plagiarist, who had helped himself to plants collected by Lewis and Clark, to the plants of Nuttall and Bradbury, and to whatever else lay at hand.

Four years later Nuttall's "Genera of North American Plants" was published and it marks a change. It is, for one thing, in English. The floras by Michaux and by Pursh are in Latin, and each uses the Linnaean sexual system of classification, with no indication that anything else is possible. Nuttall's "Genera" is also Linnaean in arrangement, but he notes in the introduction that he much prefers the "natural" system, but only for convenience uses the Linnaean.

The natural system had been first presented in 1815 to the American botanical community when the Abbé Correia da Serra gave a series of lectures on "elementary and philosophical botany" at the Academy of Natural Sciences in Philadelphia. To accompany the lectures, Correia offered a "reduction" of the genera of Muhlenberg's "Catalogus Plantarum Americae septentrionalis" arranged among Jussieu's 100 families. The lectures seem to have had little impact, and Correia was in Philadelphia, not to guide American botany

into the new age, but as ambassador from Portugal. American botanical works stuck with the Linnaean sexual system until 1826 when John Torrey turned to the natural system in publishing on plants collected by Edwin James on the "Yellowstone Expedition"; even he had used the Linnaean system in his "Compendium of the Flora of the Northern and Middle States," which appeared earlier that year.

Use of the natural system by the young man who rapidly was becoming America's most respected botanist marked the intrusion of modernity into a botany that had been developing in an isolated way for several years. During the early years of the nineteenth century there were, in addition to the collectors I've earlier mentioned, many active botanists in the United States—Bigelow and Oakes in New England; Beck, Eddy, Hosack, and Mitchell in New York; Barton, Darlington, Muhlenberg, and von Schweinitz in Pennsylvania; Charles Short in Kentucky; Elliott in South Carolina;—and Rafinesque—are a few. An amazingly long list of them is found in the "Historical Sketch" in Rafinesque's "New Flora and Botany of North America" (1837).

Many of these American botanists were known and respected in Europe, but they were all Linnaeans by training and inclination. By the 1820s botany in Europe was becoming firmly based upon the natural system, laid out by A. L. de Jussieu in "Genera Plantarum" (1789) and built upon by Brown and Ventenant and Jaume St. Hilaire. The principles of a natural system had been lucidly described and explained by A.-P. de Candolle in "Théorie élémentaire de la botanique" (1813, 1819), and were being followed by de Candolle in his "Prodromus," but in this country botany still was Linnaean pigeon-holing and that, too, was the botany being taught.

There had been earlier textbooks of botany in the United States, but from 1817 on, *the* textbook was Amos Eaton's "Manual of Botany for the Northern States" which by 1840 had gone through eight editions. Eaton was an unrepentant Linnaean and for twenty years this hugely popular textbook inculcated the Linnaean system into students of botany. There was, in addition, Almira Hart Lincoln's "Familiar Lectures in Botany," first published in 1829 (see Rudolph, 1984). Mrs. Lincoln (later Mrs. Phelps) was Eaton's protégée and the "Familiar Lectures" included the sexual system toned down for young people.

Mrs. Lincoln, in particular, sounded the trumpet of militant Americanism—". . . although Europe may boast of more brilliant stars than appear in our firmament of letters, shining with greater lustre, contrasted with the darkness and ignorance by which they are surrounded; we may justly feel a national pride in that more general diffusion of intellectual light, which is radiating from every part, and to every part of the American republic" (Lincoln, 1829). This commendable wish to spread learning throughout the republic meant, though, that Eaton and his disciples would continue to use the Linnaean system because they perceived it as being much easier to learn and much less likely to bring about uncertainty and confusion in the tyro botanist.

During the 1820s John Torrey, still a very young man, rose to the top of the botanical heap. Torrey learned his botany directly from Eaton and in his early publications followed the Linnaean system. Torrey had ambitious plans for himself; he had started in 1819 with a catalogue of the plants growing within thirty miles of New York City; in 1824 he published the first volume of "A Flora of the Northern and Middle Sections of the United States," and two years later the "Compendium" of the flora of the same area. But then in writing up James's plants, Torrey turned to the natural system and introduced it into use in America. The second volume of the Flora of 1824 never appeared—perhaps revising it into the natural system was more than Torrey chose to do. But in 1831 he presented an American edition of John Lindley's "Introduction to the Natural System of Botany," and American botany turned away, with some reluctance and with some exceptions, from the Linnaean system.

Torrey's boundaries had been much widened. He had by now set upon doing a "Flora of North America" and in 1833 went to England and to France to visit herbaria and to discuss with William Hooker his "Flora Boreali-Americana," already under way, which would cover the plants of British America. He had, too, a likely co-worker, young Asa Gray from upstate New York, showing great promise. When Torrey returned from Europe, he was prepared to go forward with his most comprehensive work in botany, the "Flora of North America," but in 1835 the State of New York resolved to organize a survey of natural history of the state and Torrey was placed in charge of the botany. He was, though, reluctant to leave the "Flora" and suggested to Gray that he begin work on some families. After initial reluctance Gray agreed and the first two parts of

the Flora were published in 1838. It was reviewed by William Darlington, physician-botanist of West Chester, Pennsylvania. Darlington had been converted to the natural system, and pointed out that, "The authors of the Flora have, of course, adopted the *natural system* as being the only one consistent with a truly scientific arrangement . . ." (Darlington, 1838).

The natural system, the modern botany of the time, was at last in place in the United States. A textbook, Gray's "Elements of Botany" (1836), following the natural system, rather than presenting it as something too complicated to learn, was available for use and would soon displace Eaton in the colleges. And an American-produced flora using the natural system was at hand.

A few years before, Torrey in Lindley (1831) had written, "The catalogue which I have prepared, embraces a considerable number of genera and species which are not described in the latest general Floras, but it is by no means asserted to be complete. There are extensive districts in North America which have never been visited by a Botanist, and even in the United States there are large spaces which are but little known or very imperfectly explored."

American botany was now ready to tackle the last major problems of the west.

George Engelmann

Although each of the three was trained as a physician, only Engelmann devoted his professional life to the practice of medicine; and this makes the more amazing the quantity of botanical work he accomplished. He was far from being a home-grown doctor who had done the botany then required in medical curricula and had retained some interest in plants. There were in the 1830s dozens of such people in this country and some interest in plants was almost de rigueur for medical men. Engelmann came to this country with a background that would have allowed him to step directly into the very top level of botanical activity—had it worked out that way. It is ironic, but quite appropriate, that it was Engelmann, coming with his sophisticated intellectual background out of the political ferment in post-Napoleonic Europe, who settled on the frontier.

He was born in 1809 at Frankfurt-am-Main, the oldest in a family of thirteen children whose parents were in the rather progressive profession of running a school for young women. The family school came on hard times and was given up in 1825 or 1826, but young Engelmann received from the congregation of the family church a scholarship that allowed him to enter in 1827 the university at Heidelberg. He was already attracted by botany for he noted in a short autobiographical sketch written in 1880 for his son that, ". . . I then began in my fifteenth year to become greatly interested in the study of plants" (Engelmann typescript at MO).

At Heidelberg he met Alexander Braun and Karl Schimper and these were men with whom he maintained life-long connections. He seems, however, to have become involved with student activists, pushing for a unified Germany, and after only one year at Heidelberg, he moved to the university at Berlin for two years, and then on to Würzburg where he graduated in 1831. The medical degree required presentation of an inaugural dissertation and Engelmann's thesis, "De Antholysi Prodromus," was a remarkable production for a young student of medicine. Engelmann was interested in morphology and the thesis deals with some teratological phenomena in plants; the word "antholysis" he explains as referring to the breakdown of—or loosening of controls over—normal developmental pathways in flowers.

After receiving the degree in medicine Engelmann went to Paris in 1832 where, as he said, ". . . in place of medical studies I found only the cholera. Still Braun, Agassiz, Constadt, and other friends were there and we led a glorious life in scientific union" (Engelmann typescript). A few years earlier some of Engelmann's cousins had been lured to settle in Belleville, Illinois, by the enthusiastic reports of a fertile midwest in Gottfried Duden's "Report of a Journey to the Western States of North America"; and the family decided that young Englemann should be sent to the new country to investigate possibilities for investment. The prospects for adventure and the opportunity to look at plants of a whole new world must have been appealing to young Engelmann.

Engelmann arrived in 1833 at Belleville and stayed in that area until the spring of 1835 when, restless, he set out through the then southwest, traveling in Missouri, Arkansas, and Louisiana, returning to St. Louis where he opened his medical practice in November 1835. Clearly this was an attractive setting for Engelmann, a small German community already established and St. Louis already recognized as the "gateway" to everything that lay beyond. So at 26, Engelmann with

the best formal training in botany—no doubt of that—on this side of the Atlantic, grounded in the modern botany of the time and with an established network of correspondents, was settled in St. Louis. Even though occupied with seeing his practice established, Engelmann continued to collect and made a point of sending plants to his correspondents in Europe.

For the rest of his life Engelmann carried on a medical practice that became so successful that by 1856 he could leave it for two years of study and travel in Europe. The medical practice, although less intensive in later years, is always there and must be regarded as background to his botany. Years later Asa Gray wrote, "They [Engelmann's publications] are the more remarkable as being the result of studies and labors aside from the preoccupations and toils of a well-filled professional life, the fruit of which would naturally have been devoted to recreation and needful rest" (Trelease & Gray, 1887). The words are those of the elderly Gray being a bit ponderous, but the point is made.

It was inevitable that Engelmann, by the twin virtues of his botanical talent and his location on the frontier, soon would joint the Torrey-Gray partnership. By 1836 Gray had become an equal partner with Torrey in preparation of the Flora of North America. Two years later came the opportunity for Gray to visit England and the continent. Gray had been appointed professor of botany at the new University of Michigan and his first commission was to buy books and scientific equipment for the university. This he did, but his own interests lay in seeking out botanists and their herbaria.

So much of the available material of American plants lay, unseen by American botanists, in European herbaria. Gray had two goals; he would get a firm grip upon this mass of botanical information that had to be mastered for the Flora, and he would open lines of botanical communication between the two sides of the Atlantic (see Dupree, 1959: 74). His first botanical call was upon William Hooker in Glasgow; here he saw a richness of plants from Canada and from the northwest and became fully aware of the great blank on the botanical map. To fill it in would be a goal for the next ten years. And Gray "met" in Europe his future friend and partner; he spent nearly a month working in the herbarium at Berlin and here he saw plants from the American midwest, collected by a Dr. Engelmann of St. Louis (Gray, 1840).

When Gray returned he was effectively unemployed for the University of Michigan was having financial problems, and the regents asked him to serve without benefit of salary, but in April of 1842 Gray was appointed Fisher Professor of Natural History at Harvard, with responsibility for the botanical garden and the promise of some freedom for research. The Flora of North America was not yet finished—it still isn't—and it would always be a weight hanging over Gray, who saw completion of the Flora as a distant goal to be reached. However, there were always other attractions, responsibilities, and opportunities not to be missed. And the partnership now was ready to go ahead.

Engelmann, Gray, and Torrey met for the first time in New York in 1840 when Engelmann was returning from Germany where he had been married. The meeting seems to have been a success; soon after Engelmann returned to St. Louis, Gray asked (12/X/1840) if it would be acceptable to name as *Engelmannia* a genus of Compositae.

Of course, there never was any kind of formal agreement among the three, but over the next thirty years there was a loose working relationship that functioned effectively. Each man had in it his place; my concern here is to examine the part played by George Engelmann during the years 1840 to 1860.

It was clear that the west already was changing. In 1839 Frederick Wislizenus, Engelmann's good friend and fellow physician of St. Louis, traveled with a fur-trading party into the Rockies and reported, "It is perhaps only a few years until the plow upturns the virgin soil, which is now touched only by the light-footed Indian or the hoof of wild animals. Every decade will change the character of the country materially, and in a hundred years perhaps the present narratives of mountain life may sound like fairy tales" (Wislizenus, 1912). George Catlin, active in the west during the 1830s, had seen with his painter's eye even more—". . . the grand and irresistible march of civilization . . . this splendid juggernaut rolling on and beheld its sweeping desolation" (quoted in McCracken, 1959).

However the changes came about, new opportunities to seize the plants of the west would develop. From 1840 onwards there was a real effort made by the three to be aware of what was happening in terms of travel in the west and to see which of the travellers might be induced to collect plants. Sometimes plants arrived almost without notice. In November of 1842 Torrey wrote to Gray that he had received a letter from "a Lt. Fremont in the U. S. service" who was

sending a box of plants from the Rocky Mountains (18/XI/1842). Torrey sent the Compositae to Gray who liked them well enough and wrote back to Torrey, ". . . Lieut. F. must be *indoctrinated* & taught to collect both dried spec. & seeds. Tell him he shall be *immortalized* by having the 999th Senecio called S. Fremonti . . ." (5/XII/1842). Such immortality was a carrot that could always be dangled before a collector.

Engelmann's immediate "job" was to keep open an eye for likely collectors on the spot—whether rich Englishmen shooting buffalo, young Germans eager to see the west, adventurers, or members of military parties. He was to watch for people; he should persuade them that collecting of plants was a good thing and might even bring a little fame—perhaps a *Senecio* named after one; and Engelmann was to show and tell the recruits how collecting was best done. So in the spring of 1841 Gray wrote to Engelmann, "You see you may be of much use to us. Meanwhile you will give me pleasure if you will tell me how I may serve you" (17/IV/1841).

Engelmann was eager, too, to make his own contributions to botany and soon became involved with *Cuscuta,* first in a long line of difficult groups that Engelmann would study over the next forty years. His interest in such groups seems to be the intellectual continuation of his early work on morphology. Current works on botany recognized in the United States only the Linnaean *Cuscuta americana,* but just in the vicinity of St. Louis Engelmann had observed several species. His first botanical publication in this country was "A Monography of the North American Cuscutineae" (1842) followed the next year by some additions and corrections. Engelmann would always be interested in these plants, although by 1849 he was writing to Asa Gray that the time had come to ". . . go at *Cuscuta* and not cease until I finish them. The thought of them is like an incubus to me—and I am almost astonished that I have not yet dreamed of a *Cuscuta* coiling itself about my limbs, etc., etc." (26/X/1849).

The system for encouraging collectors in the west went into full swing during 1843. Engelmann saw that it was necessary for a private collector to be self-supporting by his collecting and suggested to Gray that sets of plants from two such men could be offered for sale (18/I/1843). Engelmann would guarantee the quality of the specimens, which would be only of the rarest plants, and would, therefore, have to sell at eight to ten dollars per hundred. The collectors were Ferdinand Lindheimer who was farming, but not too successfully, in Texas and Karl Geyer. Geyer had been collecting in Illinois and in Missouri and now was preparing to set out for the "western and northern country." If Gray liked the plan he should place an advertisement in Silliman's Journal. Gray did like it and in the April–June number of Silliman's it was advertised that three botanists (the third was Friederich Lüders) were preparing to explore "the most interesting parts of the *far West* . . . ."

Both Lüders and Geyer would disappoint Engelmann and Gray, but Lindheimer was the most productive of the collectors active during the 1840s; dealing with his plants occupied countless hours of Engelmann's time and he wrote dozens, quite literally, of pages of descriptions and notes about the collections for Gray.

Gray was not always an easy colleague—he was impatient—he drove himself unceasingly—and he wanted more and more from the men in the field. Then, too, Gray did have field experience, but not in the west, and for Gray, comfortable on Garden Street in Cambridge, it sometimes was difficult to understand the realities of collecting on the very edge of civilization. Engelmann had to deal with Gray's demands and he simply coped with Gray's impatience by being patient with it. Occasionally there comes a hint of asperity. Writing about Lindheimer's plants, Engelmann pointed out to Gray, "Perhaps they ought to be more pressed. But in travelling and in putting up plants in a cart it is not easy to obtain the neatness required by a closet botanist. The specimens are at least as complete as possible . . ." (13/V/1845).

There was, too, competition—not here, but in Europe. During 1846 Lindheimer had a visitor, Ferdinand Roemer, from Germany, with whom he collected. Roemer returned to Germany with his own collections and a set of those made that year by Lindheimer. The plants, including Lindheimer's, were turned over by Roemer to Adolph Scheele, a clergyman and indifferent botanist, who described the new species, one hundred and thirty-nine of them, in a series of papers in Linnaea. Engelmann was angry and scornful; "And how characteristic for those persons, who seek notoriety and name with their 'mihi'—'Linum berlandieri mihi' [mihi = Scheele] and others" (Engelmann to Gray, 13/V/1849). Each article in Linnaea struck a nerve in Engelmann; he really was not interested in priority, but he *did* believe that, so far as practicable, new plants should be described in the country where discovered. On

15 February 1850, he wrote to Gray, "I think we should classify the new ones [of Lindheimer's plants] at once, so as to prevent any 'Scheeleing.'"

Englemann had become truly an American; when Gray returned from his 1850/1851 trip to Europe, Engelmann welcomed him back to "our side of the big pond" (18/IX/1851). This loyality to the adopted country made the more objectionable actions such as those of Scheele, and Engelmann reacted with annoyance to unreasonable demands made by European botanists for American plants for study. In the same letter urging action to forestall Scheele, Engelmann noted that he had earlier ". . . forgot to mention that Dr. C. H. Schultz 'Bip.' as he calls himself . . ." wished the Compositae for study; "From his letters he must be a vain and presumptuous person . . . ." Gray replied that Schultz Bip. had done good work, but Engelmann replied back, that although that might be, ". . . he is, I believe a vain and not very scientific man . . ." (17/III/1850).

In light of this it is surprising that Engelmann seems not to have complained, at least not to Gray, about Gray's inability to publish beyond the Compositae. This was Gray's favorite family, so his treatment of some collector's material always would be complete through the Compositae. But in the Candollean sequence which Gray used, the Compositae fall early among the sympetalous families, so that most of the sympetalous groups, all of the monocotyledons, and the gymnosperms, would not be written up. Gray and the others did indeed publish on many of the new things in these groups, but the unpublished families still were ripe for plucking by anyone who had access to the widely distributed sets of plants.

Lindheimer was a pleasing success as a collector—but only in Texas—and Gray yearned for the unknown plants of the southern Rockies and the Great Basin. As early as 1843 Gray had suggested that Lindheimer should be sent part way up the Oregon Trail then to work his way southward, but Engelmann gently explained that Lindheimer's home base was Texas. Gray then wanted Lindheimer to move farther westward into Texas and, perhaps, even to Santa Fe; into territory, ". . . where I trust many of his plants will have no Latin names until we christen them" (Gray to Engelmann, 3/II/1845). Lindheimer stayed in east Texas and even married; Gray fumed, "Send me the new Lindheimer plants as soon as you get them and *stir him up*. Can't you send a collector to Santa Fe?" (Gray to Engelmann, 27/II/1846).

However, within a few months' time, the second great success as a collector would be in the field. War with Mexico was declared in May 1846, and Gray saw at last an opportunity to send a collector to Santa Fe with the army. For a moment Gray might have considered going himself, but Engelmann was commissioned to find in St. Louis a collector. He found Augustus Fendler who received free passage with the army and Engelmann saw this as a good sign for science in the United States (Shaw, 1982). Engelmann was always a republican, but he doubted whether a republican form of government was best suited for the promotion of science.

Fendler spent several months in Santa Fe and returned with beautiful material that pleased Gray very much. But Engelmann again had to devote hours of the time left from his medical practice, to work with Fendler in arranging the sets for sale, and to deal with Fendler himself.

The Texan plants from Lindheimer were described by Engelmann and Gray as "Plantae Lindheimerianae," the first part published in 1845 and the second in 1850. The third part would not appear until 1907 (Blankinship, 1907). The amount of work done by Engelmann on Lindheimer's material truly is amazing—during the middle years of the 1840s he sent to Gray dozens of closely written pages of descriptions and of notes on the plants. There was, in addition, the labor involved in sorting out the material into sets and then the worst, perhaps, of all, acting as banker.

One goal, after all, was to sell or exchange sets of plants in the hope that the collector could be nearly self-sufficient. Gray in the east served as "distributor" of the sets and dunned the purchasers for payment. So Gray to Engelmann in December 1849, "I have written a *very strong* letter to Brown [Robert Brown] (who was in Ireland at last accounts) to send on the cash for Fendler—I think he can neglect no longer—but he is a slow and indolent old sinner." The monies eventually received would then go to Engelmann who saw that they reached Lindheimer or Fendler, but often Fendler would be living on what Engelmann could afford from his own pocket.

Lindheimer and Fendler were the collectors

who occupied most of Engelmann's free time during the 1840s, but he was also involved with Josiah Gregg, Fremont, Gordon, and collectors of lesser significance. At times Engelmann despaired of doing all that he wished; he wrote to Gray, "How often have I thought as you, if I could only multiply myself to do all that I have before me—how often cursed those numberless fellows, who do not know how to kill their time—which would be so eminently valuable to others!" (11/II/1847).

Fortunately, after Lindheimer and Fendler, collectors and their plants made fewer demands upon Engelmann's time—times, in fact, were changing. From the mid years of the 1840s collecting in the west turned from the hands of private individuals, such as Lindheimer and Fendler, to those of government-sponsored collectors and of military men. In 1846 Major William Emory made a reconnaissance from Fort Leavenworth to San Diego, and although Engelmann helped with botanical preparations, the plants went to Torrey and Gray. Charles Wright collected in Texas during the 1840s and then went with the post-Mexican War Boundary Commission, but his botanical contact was Asa Gray and the overall botany of the Boundary Survey was finally prepared by John Torrey. During the 1850s collecting in the west was done by the parties carrying out the railroad surveys and, again, those plants went to Torrey.

Torrey and Gray saw that Engelmann's botanical abilities were being wasted by the drudgery of sorting out plants and writing lists and wrapping parcels; and Torrey in particular urged Engelmann to concentrate upon some genus or few genera that he might prepare for the Flora of North America. No matter how much time was taken by the flood of material from the west the unfinished Flora still made its own demands. In 1850 Engelmann remarked to Gray, "I am glad to see that both your northern flora and textbook are in our bookstores and are bought—But you forget the flora of N. America!!" (16/IV/1850).

A group that appealed to Engelmann, with his keen eye for the interesting and the difficult, was the cacti now coming in great numbers from the west. From 1846 he published on the cacti of every collector and expedition and by 1856 Engelmann had prepared a "Synopsis of the Cactaceae of the Territory of the United States and Adjacent Regions," in which he recognized 117 species where only a few years before "scarce half a dozen had been known." The cacti were the best group Engelmann could have chosen—he was close to the field, so that plants, including living ones that could be grown in the family garden, could be sent directly to St. Louis. And Engelmann knew where problems lay; "The study of the Cactaceae has been too much in the hands of gardeners and amateurs" (Engelmann to Gray, 13/IV/1855).

The 1840s were an exhausting time for Engelmann with botany piled upon his medical practice, especially when cholera swept through the city. During the winter of 1848/1849 and into the autumn of 1849 the epidemic of cholera was especially severe. In May Engelmann told Gray that, "We are in a state of war here; day and night on our legs—fighting the great destroyer, the cholera—of course no room for anything else, not even for sleeping or eating comfortably—like soldiers before the enemy. I like the excitement which it is for me" (12/V/1849). Yet the very next day, he wrote again to Gray, filled with annoyance about the shoddy work of Pastor Scheele on the plants of Roemer and Lindheimer.

Eventually, though, the strain showed. In the summer of 1851 Engelmann took off from medicine for a few days to attend the AAAS meetings in Cincinnati; and as he told Gray (29/VII/1851) it was, after eleven years of "slavery" in St. Louis, a marvelous break—making new friends and meeting again old ones—Louis Agassiz, for one—nearly twenty years after the summer of 1832 in Paris. Gray was concerned and asked when Engelmann could retire from medicine—for the greater good of botany.

The reply was, of course, that his patients needed him, but Engelmann had started to think about change. When the railroad survey parties were set up in 1853 he considered seeking an appointment with one, but decided against it. "I should probably prefer to be independent" (Engelmann to Gray, 4/VI/1853). The thought lingered though, and a year later Engelmann "half thought" about going with Major Emory to Sonora, but he had heard about it too late; he told Gray though that, "I must have some relaxation and reanimation after a steady medical practice for 14 years" (Engelmann to Gray, 18/IX/1854).

Fortunately the change was not far away. In May of 1856 Engelmann mentioned to Gray that he had met Henry Shaw. Shaw, intending to found a garden in St. Louis, had asked Sir William Hooker to recommend someone who might

organize the garden and Hooker replied that the very best man was right at hand in St. Louis. Engelmann had already planned a visit to the east and on to Europe and in November 1856 the family sailed. During the fifteen months abroad, Engelmann bought books and the Bernhardi herbarium for Shaw's garden and studied *Cuscuta* and cacti, so that in 1859, *Cuscuta* was at last laid to rest with a "Systematic arrangement of the species of the genus Cuscuta, with critical remarks on old species and descriptions of new ones."

Engelmann practiced medicine to the end of his life, but after the trip of 1856–1858 at a more leisured pace. Exploration, too, had changed very much, and Engelmann no longer had to deal with the privately operating collectors. The consequence was that during his last twenty-five years Engelmann was able to carry on with the kind of carefully done and detailed work begun with *Cuscuta* and the cacti, and even to travel with the chance to see his plants in the field. Again, this list is not inclusive, but after 1860 Engelmann was able to produce major works on *Vitis,* on which he would publish nearly to the end; on *Yucca* and *Agave,* on *Isoetes,* on *Euphorbiaceae* and *Asclepidaceae,* and, most elegantly done, treatments of *Quercus* and of conifers. He could also produce, to the tune of forty pages' length, "A Revision of the North American Species of the Genus *Juncus* with a Description of New or Imperfectly known Species." The paper opens with one of the longer, but most appealing sentences in any systematic work, and one which tells much about the man.

> The difficulty I found in arranging the species of *Juncus* of my own herbarium, the doubts in which the authors left me by incomplete and unsatisfactory descriptions, and by confusion in names and synonyms, the want of confidence which all my correspondents, even such as had paid a good deal of close attention to it, seemed to place in themselves and their own judgement when this genus was under dicussion—all this induced me to enter upon a critical study of our *Junci.*

Engelmann tended to be a splitter—often Gray would chide him for splitting, while admitting that he, Gray, tended to lump, but Engelmann never just poured out new species. And conspicuous in his monographs and revisions is a careful effort to array the species in some pattern of relationships. Certainly he was not always successful, but Engelmann sought always to present a finished product. The kind of work that Engelmann did is impressive, and the happy combination of quality and quantity of his work is amazing. After Engelmann's death, Henry Shaw asked Gray and William Trelease, then director of the Garden, to prepare a collection of his botanical publications (Trelease & Gray, 1887). The collection, which is not quite complete, produced a book three inches thick.

Engelmann arrived just as the frontier was moving beyond St. Louis, and he spent only a few more than ten years being directly involved in the "processing" of plants coming from Lindheimer and Fendler. His contributions, though, during the 1840s toward making the west botanically known were substantial, and he was the perfect frontier collaborator for Gray—patient, willing to spend the hours needed for turning bundles of plants into specimens for an herbarium and then into publications; and a very good botanist. Valuable as was this work, though, his contributions to American botany through his monographic and revisional publications are still more important—these set for young systematists a standard of American-produced taxonomic excellence.

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AUGUSTUS FENDLER (1813–1883), PROFESSIONAL PLANT COLLECTOR: SELECTED CORRESPONDENCE WITH GEORGE ENGELMANN

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ABSTRACT

Augustus Fendler, a German-American interested in speculative physics, meteorology, and botany, was the first person to collect plants in the area around Santa Fe, New Mexico, in 1846. His life can be partly documented through his correspondence with George Engelmann and Asa Gray, both of whom esteemed Fendler's friendship and expertise as a plant collector. Many of Fendler's letters to Engelmann were written in German; the originals at the Missouri Botanical Garden have been translated into English by the second author and were used extensively to create the following biography.

During the nineteenth century a small number of people who preferred to seek their livelihood far from the madding crowd chose the arduous life of the plant collector. Although the hardships of this *modus vivendi* attracted some, the exploration of nature's diversity—and doing so at one's own pleasure—lured most. For Augustus Fendler the quest for plants provided a haven for his "painfully diffident" personality and inquiring mind (Canby, 1885). His philosophy practically coincided with that of his more famous contemporaries, Emerson and Thoreau, as may be seen in Fendler's privately published "Mechanism of the Universe" and in his letters. Despite his shyness or perhaps because of it, Fendler won the lasting affection of William Marriott Canby, Asa Gray, and George Engelmann. In their own ways these three persons contributed greatly to floristic botany in North America during the 1800s. Fendler enriched the herbaria of all three as well as those of others who purchased sets of plants from him.

The summer following Fendler's birth on 10 January 1813 in Gumbinnen, East Prussia, his father died, but he soon acquired a stepfather. Although for some years the boy attended school, he eventually had to leave because his family could not afford the tuition. Apprenticed to the town clerk, he soon found this a "spirit-killing employment," and when given the opportunity to accompany a government physician on an inspection tour of cholera quarantine stations along the Russian border, young Fendler volunteered, even though he had to clerk for the doctor (Canby, 1885). When Fendler returned to Gumbinnen, he learned the tanning trade, hoping that this would allow him to earn a living anywhere he might travel. Tanning, however, so exhausted and, at times, nauseated the frail youth that Augustus decided to enroll in the Royal *Gewerbe Schule,* a polytechnical school in Berlin. But after one successful year there, the daily schedule had so drained his strength that in the Fall of 1835 he withdrew. Following a period of wandering in German cities, he sailed from Bremen for Baltimore, Maryland, in 1836. With little cash in his pockets he sought and found work in a tanyard in Philadelphia, but he quickly abandoned that for lamp manufacturing in New York City, which proved to be a more profitable occupation in lean years ahead. However, the money crisis and panic of 1837 so depressed the business that he was forced to quit the factory in the Spring of 1838. Even before the hard times of 1837, Augustus had read of the opportunities to be found in St. Louis and the Far West.

After thirty days via canal-boat and steamer from Albany through Buffalo, Cleveland, and Portsmouth, Fendler finally reached the Mississippi city of 13,000 people. He worked for a time with a man "who had just commenced making spirit-gas for lighting public houses, as the manufacture of coal-gas had not reached so far west" (Canby, 1885). The prospect of working through the winter in an unheated room so discouraged Fendler, however, that he departed for the South shortly before Christmas in 1838, knapsack on his back. He walked through the forests of southern Illinois, the canebrakes of Kentucky and part of Tennesssee before meeting two other wayfar-

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ers. The three bought an old skiff just below the Ohio River's mouth and managed to float a good distance before finally sighting a steamboat that had broken through the winter ice upriver. His inborn wanderlust urged him westward; so he left New Orleans for Galveston, Texas, in January 1839. Not finding Galveston particularly inviting—he described it as "a dozen poor-looking houses scattered about its low and sandy surface" (Canby, 1885)—Fendler tried Houston. He explored the area and almost settled there, which would have been simple under the immigrant land grant law, but he had no interest in fighting Comanches for the right to secure his claim. After he returned from the then unsettled area known as Austin the ravages of yellow fever that greeted him at Houston clinched his decision. His wallet empty and his body fever-weakened, Fendler was forced to retreat north to Illinois, where he taught school for a short time.

At this time, possessed by a particularly acute case of transcendentalism, Fendler wrote in his own "autobiography" (referring to himself in the third person) something akin to Thoreau's *Walden*:

> Autumn in North America, and especially in the Western States, always presented more charms to F.'s mind than any other part of the year. Hence in 1841, when autumn winds began to scatter the falling forest leaves, he was seized with an uncontrollable desire for solitary life in the wild woods, removed from the haunts of man, in short, for the independent life of a hermit. In his search for a proper place, he came upon a little village called Wellington, situated on the banks of the Missouri River, three hundred miles above St. Louis. Here he learned that an uninhabited island, two and a half miles long, called Wolf's Island, not very far below the village, was at his service.
>
> Without delay, F. packed his little baggage, including some bed-clothes and cooking utensils, a rifle, an axe and some books, in a canoe, also taking along some provisions, and started for his new home. This island was densely wooded with gigantic trees. On the lower part of it, farthest removed from the village, was an old, dilapidated log cabin, the former abode of some woodchoppers. The upper part of the chimney was gone, so that a tall man standing on the outside of it could look down inside upon the low fireplace, from the burrows of which wild rabbits popped forth at the approach of man; part of the roof was gone, and the door carried off. There was plenty of game, however, especially wild turkeys. These latter had chosen the island as a roosting place for the night and as a place of safe retreat in daytime when chased on the mainland by hunters. In a so-called "turkey-pen" they were easily entrapped, and thus an abundance of excellent food secured. To return the borrowed canoe to its owner and to make one of his own was his first aim. So he went to work at a big trunk of a prostrate tree, and with an axe shaped part of it into proper form of a light canoe eight feet long.
>
> Removed from the crowd, the hum and strife of men, his pastimes consisted alternately in trapping, hunting, reading, musing and meditating, and on mild and sunny days in paddling up a placid arm of the river, then turning round lean idly back in his canoe, thus floating home again. Occupied in this way F. lived for about six months, enjoying the sweets of solitude with a satisfaction of inward peace of mind and bliss higher than he had expected—contented and happy as ever mortal man, similarly situated, can claim to be. His feelings of content would at times culminate into feelings of thankfulness, which then found vent in words akin to the soliloquy of Faust at his forest cave: "Spirit sublime! Thou unto me gav'st ev'ry thing I pray for."
>
> Only once he met on the island with a human being, namely, with its owner, coming to see him. How long F. would have continued to live here is hard to say, if the great spring rise in the Missouri River, which began to overflow part of the island, had not taken place. When its waters rose to within a short distance of his cabin he thought 'twas time to leave, and entrusting himself and baggage to his frail canoe, was hurried along at no mean speed by the precipitate rush of the foaming and rapidly swelling stream. Dodging floating logs and broken ledges of ice, he expected every moment to be swamped by the high waves caused by a stiff breeze blowing up stream. To land his tiny craft admidst eddies and whirlpools at Lexington, ten miles below the island, was, how-

> ever, the most perilous part of the venture (Canby, 1885).

While the somewhat utopian life of an ensconced hermit always attracted Fendler, a fascination for travel constantly lured him away from it. In 1844 he returned to Germany for a visit home. A Koenigsberg professor of botany, Ernst Meyer, aroused Fendler's interest in plant collecting. Encouraged that he could make a decent living by collecting plants and selling the specimens to foreign herbaria, Fendler returned to St. Louis, this time with his brother, and began in earnest to collect as the seasons changed, between Chicago and New Orleans. He took his excellently prepared plants to the local expert, Dr. George Engelmann, whom he had met the year before, for identification. When in Houston Fendler had first learned of plant collecting from one of Engelmann's collectors, another German, Ferdinand Jacob Lindheimer, but he had thought nothing more of it as a profession until Ernst Meyer had suggested it. Lindheimer warned him of the hazards of life in the untamed West, where he would have to conquer plains and mountains, drive a wagon, survive on buffalo meat or worse rations, live in the saddle or walk twenty miles a day, and occasionally fight for his life against the natives. Lindheimer, Fendler and others who accepted this vocation never had time to learn enough botany to work on their own collections, but they developed a keen sense of the new and unusual, which profited science in the end (Dupree, 1959: 156). Plying their trade, these pioneers for botany steadily grew unused to the discipline and courtesies required in civilized life, so they generally could not stand the cities for long, but sought refuge in the country. This, of course, suited Fendler's shy and retiring nature perfectly.

In time, Engelmann and Fendler became fast friends. The doctor recognized Fendler's botanical promise and communicated such to Asa Gray. The latter, who never lost an opportunity to get plants from the Far West when he could, secured a letter from the Secretary of War, authorizing the Army, then at war with Mexico, to provide the collector with free transportation and provisions to Santa Fe and back. Since his was the first botanical trip in that part of the country, it has recently been the focus of some historical attention (Shaw, 1982). Gray's *Plantae fendlerianae novi-mexicanae* (1849) appropriately accounted for this classical plant collection.

Engelmann's keenness for cacti brought observations from his new field collector, which incidentally highlights one of the many problems faced by the field botanist in obtaining specimens of large succulent plants. On 8 November 1846, this from Santa Fe:

> Cactaceae can be found here in large quantities, however, barrels and cases to send them in are very hard to obtain even at the highest prices. You just cannot imagine the lack of wooden boards here; the volunteers have to use the boards of the wagon bodies in order to make caskets for their dead, and empty cases are sold by most of the merchants according to weight for 12½ cents per pound. With great efforts I was able to obtain an empty sugar barrel from the Commissary for my collected Cactaceae.

Meanwhile Gray had received some of Fendler's specimens from Santa Fe and wrote to Engelmann that Fendler had to go back, because his specimens were excellent. Gray said that they would sell well, too, but lamented that if only Fendler had known more botany, he would have eschewed the "common plants" and bestowed his labor on the new ones abounding there. However, Engelmann had already perceived his collector's shortcomings and was training him. No lack of enthusiasm for "herborizing" discouraged Fendler from another trip to Santa Fe. Only basics deterred him, as he told Gray:

> When my pecuniary means at Santa Fe were nearly all exhausted, when I had to sacrifice one thing after another of my most necessary effects, to keep up a few days longer the scanty support of our lives [his brother accompanied Augustus], in order to collect something more of the vegetation of that region, I looked forward with utmost confidence to those gentlemen in the East, who had induced me to go out to Santa Fe, and who would, as I hoped, leave me not without assistance as soon as I should have returned with my collections to St. Louis. It was this hope that made me bear all the difficulties most cheerfully under the happy impression that the enjoyment of the fruits of my labour would soon compensate for all.
>
> But alas! It was to be otherwise (McKelvey, 1955).

Unfortunately Fendler had to borrow money

for sustenance while sorting the nearly 17,000 plant specimens into salable sets. His brother, also broke, enlisted in the Army. As Fendler explained his plight further:

> I have expended about 200 dollars of my own money; but I gave up a business in which I was doing well, and in which I cannot at present engage again for want of means. To this may be added the sad prospect I have now before me, that by the time I shall receive some money, this money will be nearly all wanted to pay my debts which I had to contract during all this time (McKelvey, 1955).

By now Fendler knew what others doing likewise discovered, namely that plant collecting was neither the profitable nor glamorous occupation that it was sometimes thought to be. Nevertheless, Fendler resolved to try Santa Fe again, but the ensuing debacle marked his last traffic with the military.

In June 1849 ten wagon-loads of people from Wisconsin en route to California joined the Army caravan at Fort Leavenworth, Kansas. On 26 July Fendler wrote Engelmann (in English) that he had been thwarted constantly by one Captain Morris of the Mounted Riflemen whose orders Fendler's teamster had to obey. On 13 June, shortly after noon, a thunderstorm drenched the party.

> We proceeded nevertheless on our journey, and the wagons soon after commenced to cross a creek (a branch of the Nemahah River). After a part of the train had passed the creek, the progress of the remaining part was stopped as I understood by the commanding officer for more than an hour, and then ordered to proceed again, while during all this time the rain was pouring down. My teamster accordingly drove on into the bed of the creek in which at this time the water was only about 18 inches deep.The wagon next before us after crossing the creek stopped for some reason or other a few minutes in getting up the bank, and my wagon was hereby prevented from going on, and obliged to stop for 5 or 6 minutes in the creek-bed. During this short interval the water in the creek began to rise very fast and all at once the back water came rushing *up* the stream with such fury as to carry logs and branches before it. The wagon that had detained us now started ahead, but alas! it was too late for us to follow, for the mules were already swimming and all that my teamster, who was a most expert swimmer, could do was to jump into the water and cut loose the mules as soon as possible. But they got entangled in the harness and were fearfully struggling for their lives. At the risk of his own life the teamster succeeded at last to cut them all loose. One mule however died in the water, another one died the next morning and the remaining four had suffered so much from the swallowing of water, that they were in a very enfeebled condition. The water soon rose to the middle of our wagon cover far above the load. During all this time there was a number of regular soldiers and of teamsters idly looking on, smiling and wondering at the novelty of the scene. All they did do was to holler to the teamster to come out, save his own life and let the mules be drowned, but they did not even lend me a hand in pulling out the mules. My own efforts to rescue anything of baggage from being soaked by the water were too feeble, and in the attempt I came near losing my life . . . . The wagon was then abandoned to the creek. When the water had somewhat run down we unloaded most of our things, and after the rain had ceased next morning I was at the doleful work of opening and unpacking all my trunks, boxes and provisions-bundles, to spread and strew everything to the open air, and to wash the settled mud from blankets, clothes, books, paper and a hundred minor articles.
>
> There was not a single thing that I had been able to get out before the water had soaked it, and you may judge of the loss and damage in this unfortunate event. I had laid in a stock of provisions at St. Louis for at least 6 months for two men [Augustus and his brother]. Of these provisions the sugar was nearly all dissolved, the coffee soft enough to press it flat between my fingers; into the flour the water had penetrated from 1 to 2 inches all around the sacks. I had to throw away nearly all of hard-bread, cornmeal, tea, rice, etc. Most of the medicines you kindly had put up for me were destroyed. Not to say anything about the great number of articles that were now covered by rust or otherwise damaged I will only mention here 14

reams of brown paper that I had taken along for the purpose of drying plants. Every one of these reams after being taken out of the water had its weight increased to such a degree, that I was barely able just to lift it off the ground. The creek was still too deep next day to ford it, and several wagons being on our side of the creek, Capt. Morris was obliged to lay by next day, which was a happy circumstance to me as it gave me an opportunity at least partly to dry some of my soaked baggage. A few days later, all my books had lost their covers and the leaves moulded and partly rotten for want of sufficient time in drying. But what pained me most was to see the greater part of the 1000 specimens of my Santa Fe plants that I had so carefully with so much labor and patience pasted on paper and bound to book form, fall rotten from the moulded leaves [of] the book. This was a loss that could not be restored again by money . . . .

All the plants (about 180 specimens) that I had collected during my stay about Weston, Fort Leavenworth and on the journey up to the day of disaster were completely decayed and had to be thrown away.

On 25 June Fendler reached New Fort Kearney on the Platte River at the head of Grand Island, about 300 miles from Fort Leavenworth. Although he had hoped to reach the Great Salt Lake, the condition of his mules would not allow it. For some reason Capt. Morris would not permit an emigrant to lend two mules to Fendler so his team could manage the load. After several unsuccessful negotiations with other emigrants, Fendler reluctantly joined a small Government train of three ox-drawn wagons returning to Fort Leavenworth. The Quartermaster there offered Fendler passage to Fort Laramie whence he would have to find his own way to the Great Salt Lake, but the time for this journey would have put him at the Lake in winter. "For the present," he informed Engelmann, "I only hasten to inform you of the failure of my expedition." Asa Gray, who had encouraged him to try for the Lake, sympathized with Fendler's temptation to abandon plant collecting and seek his fortune with the other forty-niners heading for the gold discovered at Sutter's Mill, for he would certainly "make more at digging gold than he ever can with plant gathering" (Dupree, 1959: 164). And Fendler was sorely tempted.

When Augustus finally arrived in St. Louis, however, he was overwhelmed by yet another series of mishaps: All his plant collections, books, travel journals and other worldly goods had been destroyed in the "Great Fire" that had swept St. Louis during his absence. This should have been enough to send him back to the lamp factory, Wolf's Island, or San Francisco. Instead, on 4 December 1849 he boarded the steamboat *Uncle Sam* bound for New Orleans, and after obtaining necessary supplies at Engelmann's expense and after fitful starts, Augustus and his brother finally sailed from Louisiana to Chagres, Panama. Between rainstorms they managed to collect some plants, but were finally driven back to New Orleans on 20 April 1850. [Fendler's field notes for his Panama trip are at US (see Stieber, 1982); his other field records are evidently lost.] "I hardly believe that there is any other part on this earth where there is so much rain and where the rainy period is comparable to that of Panama," Fendler, now settled in Camden, Wachita County, Arkansas, wrote Engelmann on 1 May. Since leaving St. Louis the previous year, the Fendlers had spent $274 and were debtors once more. So Augustus begged Engelmann to buy his entire set of plants and peddle them from St. Louis. Meanwhile the brothers tried to raise some money from vegetable and fruit gardening. Fendler also had some insects that he wanted to send to J. L. LeConte in New York and asked Engelmann to arrange it.

He had progressed in his study of botany enough to remark to Engelmann that "the southwestern part of Arkansas where I am now may have much of interest for botany; and the flora of this area is probably a transition of the Texas flora to the middle states." Fendler also asked for books, Gray's "Illustrated Genera" and Michaux's "work about the North American trees." The sojourn in Arkansas was aborted by unproductive soil, which meant that "cash was very rare."

In June the Fendlers moved back to New Orleans, where Augustus added Gray's "Botany of the Northern United States" to his library, and it cost only seventy-five cents! In July they resettled in Memphis, Tennessee, and prospered there for the next four years by operating a gaslamp business. It pleased Fendler to learn that Engelmann and Gray intended to name a plant after him. (*Fendlera* Engelmann et A. Gray, a new genus of Saxifragaceae, was published in the *Smithsonian Contr. Knowl.* 3: 77, 1852.) Fendler

conducted horticultural experiments in Memphis, sowing seeds of plants that he had collected in Chagres and of others that Engelmann sent him. Four species from Chagres grew well, of which "two beautiful mimosa species (both bog plants) are now 4–5 feet high, but probably won't last very long outside" (28 September 1851). By this time Fendler had already recorded temperatures of 38 degrees and observed frost on the leaves. Meanwhile the chemical-oil business was succeeding so well that Fendler had to abandon collecting and also most of his reading. The latter enjoyment had so increased his proficiency in English that by the 1870s he had translated Goethe's *Faust* into English verse (Canby, 1885), presumably for his own pleasure.

Fendler reported his exact observations on the growing plants to Engelmann and his daily meteorological measurements to the Smithsonian Institution. "I found that the thermometric studies made by the local Navy-Yard here and sometimes published are very different from mine," he wrote on 1 March 1853. In fact, he continued,

> during a whole month not one single item agreed with mine. Only one example: 3rd February 1852
>
> | | sunrise | 3 p. m. |
> |---|---|---|
> | according to my observation | 28° | 64° |
> | Navy-Yard— | 47° | 48° |
>
> There seems to be no difference between the thermometers themselves since on the 19th of January 1852 both showed at sunrise −2°F . . . So much for official meteorological statements of the local Navy-Yard

Meanwhile his gas-lighting business began losing customers. By 22 February 1853 the Memphis Gas Company was supplying many residences and businesses with natural gas, but Fendler had known of the impending introduction of gas-lighting in Memphis the previous September, at which time he had planned tentatively to convert part of his business to the distillation of alcohol. Although on 15 August 1853 Fendler expressed some interest in exploring the Great Plains with Engelmann, he had already determined to move farther south to a German settlement in Venezuela known as Colonia Tovar. Business had declined too much for him to remain any longer in Memphis, but he told Engelmann that his main reasons for wanting to move to the village near Caracas were:

> In a city with a population of 70,000 I believe to be able to find more security than here, and secondly, because I believe I shall have a better climate there. Then also, the wish to live again in a mountain valley and to be in the vicinity of a rich mountain flora! without having the difficulties of long and difficult communication as I found in Santa Fe . . . . I should think that the mountain area of Caracas should be rich in cactus species [15 August 1853].

Always eager to please Engelmann, Fendler also noted that the *Opuntia* plants that he had sown for him grew "very slowly" in his Memphis garden.

By 16 December 1854 the Fendlers had relocated to Colonia Tovar and were preparing nearly eight cases of specimens for Engelmann, including fifteen to twenty specimens each of 250 fern species and of six palm species. "You can imagine how much work this involves," Augustus explained. "However, Lindley's Vegetable Kingdom is a great help to me . . . [and] apart from the ferns, the colony contains orchids, Solanaceae, Rubiaceae, Melastomataceae in great numbers of species." Meanwhile, he continued his meteorological observations, later receiving a barometer and dry and wet-bulb thermometers from Joseph Henry (Fendler to Engelmann, 27 April 1856). The description of the conditions that Fendler left behind in the United States would make any current weather report of the same area sound humdrum:

> There is [at Colonia Tovar] no scorching summer's heat, no fearful winter's cold, neither tornadoes to devastate the country, nor gales to blind the inhabitants with sand or dust, or penetrate their clothes and flesh with piercing frost. Lightnings are rare and rather harmless, thunders merely grumbling (Canby, 1885).

The Fendlers designed a fountain next to their house, hollowing out a palm trunk and propping it so that the water could shoot up to nine feet in the air. Besides apple trees, bananas and palms, a vegetable garden provided them with potatoes and other staple foods. But since cash for sale of plant specimens merely trickled in from his friends in North America, Fendler resumed distilling alcohol to earn some income. Engelmann's letter of 27 March 1856 heartened him with the news that a natural history society and a botan-

ical garden (Shaw's Garden) would soon be founded in St. Louis. "The reason I hope to end my life in the United States," Fendler wrote on 1 April of that year, "is the wish to follow the results of intensive scientific education. From the last I feel so far removed in Venezuela and in this regard I am very isolated."

During Fendler's visit to the United States later that month, Sullivant paid him for sets of mosses and liverworts; Tuckerman did likewise for lichens. However, LeConte would not buy Fendler's 600 "bugs" even though the entomologist thought them admirable specimens. He bought "only North American things. Therefore," wrote Fendler, "I shall keep them for myself."

By the time the Fendlers returned to St. Louis in 1864, Shaw's Garden had already been thriving for five years. Soon after arriving, the brothers established a small farm at Allenton, Missouri, not far from the city, and lived there for seven years. Augustus, however, did accept a short-term offer from Asa Gray to work as a curator at Cambridge, one of many abortive efforts by the elder botanist to alleviate his workload (Dupree, 1959). The negotiations began nearly a month after Abraham Lincoln's assassination and culminated in Fendler's move to Cambridge. He described his routine to Engelmann (2 November 1865):

> During the day, which begins at 7½ in the morning until 5 o'clock in the evening, I work in the herbarium here where there is always work to do and of the *four* working days of which Gray wrote me earlier, nothing is said any more. I did not claim any time for myself, since I well know he would like me to lose as little time as possible. I did the sorting of Ranunculaceae to Rosaceae inclusive, according to the partly published work by Benth. and Hook. "Genera plantarum" and numbered the genera accordingly. The grasses according to Steudel; Labiatae, Scroph., Verb., Solanaceae, Compositae etc. according to DeCandolle. At present, I am working on the Cyperaceae. Gray still has a great number of bunches of dried East Indian plants from the Kew herbarium. Furthermore, several packages of Japanese plants: collected by Oldham, which will still have to be poisoned and pasted on white paper. Then, the plant parts of Wilke's expedition have to be looked at, labels to be written for the duplicates. Furthermore, many plants, before being laid out for pasting, should be compared with those in the herbarium, whether there is still room on the old sheets and whether already a sufficient amount of specimens of one and the same species in the herbarium, in which case Dr. Torrey receives the duplicates. Also there are other collections to sort, for instance my own and that of Wright. From time to time, I also plant something small in the garden, keep the rooms of the herbarium clean, get charcoal out of the basement, etc. . . . Gray learned yesterday that the gardener demands $5 per week for my board, he had only counted on $4 at the most and does not want to give more in the future; and therefore I again have my meals at Gray's table where the midday meal is served at 5½.

This never worked out well because Fendler felt it a hardship to have to shave and dress well in the presence of "ladies" and because he preferred to eat alone. Gray accommodated Fendler's shyness and paid for his meals at a local boarding house.

Meanwhile Fendler had been considering two scientific topics, the theory of heat and the cause of fluctuation of barometric pressure from hour to hour that he had noticed in Venezuela. His lucubrations gave rise to the following remarks to Engelmann on 4 February 1866:

> When I sent Prof. Henry my meteorological observations from Venezuela in June 1857, I sent them together with the half-hourly barometer readings and stated my theory about the cause of the periodical differences of the barometer . . . . In the report of the Smithsonian Institution of 1857 in which my observations and letters were published, this theory was left out, probably because Prof. Henry thought it too daring. Now, I find in one of the numbers (no. 114, p. 380) of the Journal of Science and Art that a Mr. Chase from Philadelphia arrived at the same result after three years of continuous hourly barometrical readings made by the request of Sabini during the years 1842–45, and proves this with a large algebraic account. The same will probably happen to my theory about the warmth [heat] if I cannot publish it soon.

Dr. Gray says I should write to Henry and ask him to return my manuscript in order to prove the priority of my theory.

[On 25 December 1865 Fendler had written Engelmann about the "warmth":] Gray obtained for me "Tyndall's Lectures on Heat considered as a mode of Motion" and I spent many evening hours reading this. I found that the experiments were carried out well and with great ingenuity. But the author did not succeed in proving that heat is nothing but a "mode of motion". I have several notes and could show direct contradictions and that he gets sometimes involved with problems from which he cannot extricate himself. I have never been able to see that warmth is something *material*; but neither can I believe that it is nothing but motion. I believe in my own opinions which I have not yet found in any work and intend to develop them later on when I am back home and have more time.

In Spring 1866 Augustus returned to help his brother farm at Allenton and continue his friendly collaboration with Engelmann. Unfortunately, he discovered that in his absence, his brother had developed night-blindness. In the summer of 1871, the brothers sold the farm and moved into St. Louis, an action that he later regretted because he found so few people there with whom he shared any interests. He loathed the city principally, he said, because of "the horrible noise, din and hurry of men adoring mammon." The wandering life of a collector certainly had turned him against city dwelling, too. St. Louis disagreed with him so much that he and his brother decided to visit Gumbinnen, Germany, in 1872. It was to be an extended vacation to judge from the four boxes of books they took with them.

However much he disliked living in St. Louis proper, his first letter to Engelmann from Germany indicated that Augustus Fendler missed the United States. Although the weather in East Prussia was exceptionally mild in 1872—so mild that he compared it to the idyllic Colonia Tovar—"Most everything here is more expensive than in America [and]," he continued to Engelmann (2 January 1873), "we don't like the still ever-present narrowminded spirit of the bourgeois, the soldier and officials, and my capital is not sufficient to live on." So Fendler planned again to return to America and bolstered his botanical knowledge by visiting the remarkable botanic gardens at Koenigsberg and Berlin. The former boasted its fine collection of aquatics, especially the attractive species of the Nymphaeaceae, whose foremost student, Prof. Johann Caspary, greeted Engelmann's friend with warmth. Professor Alexander Braun, a notable phycologist, drove Fendler through the Berlin garden where the young collector "was pleasantly surprised to see the large collection of living cactus plants with their strong and healthy growth." Braun also informed him that George Engelmann, Jr. had passed his doctoral examination.

On 4 April 1873, after only eleven months in Gumbinnen, the Fendlers left for Hamburg. They sailed with some 500 other passengers, mostly Scots and Irish, on the *Ismaila,* which arrived on 1 May in New York, one year to the day after they had disembarked at Hamburg. Finding that John Torrey had recently died, the Fendlers continued on their way to Philadelphia where Augustus renewed acquaintances with LeConte and Thomas Meehan, both of the Academy of Natural Sciences. Here Fendler planned to present "some small scientific papers" and so settled temporarily in the city. Again he grew restless and tired of city life and after some exploration of the environs of Philadelphia found lodgings in the rustic town of Seaford, Delaware, on the shores of the Nanticoke River. Seaford had "a bank, two hotels, three churches, one mill and two sawmills," and one other German. The oyster trade was "blooming" there, as Fendler wrote Engelmann on 16 February 1874.

The plants of the Coastal Plain, a phytogeographic region new to Fendler, interested him. He was especially startled to find that "this sandy and sterile looking soil can produce such huge oak trees as I have seen myself." Besides an income from interest on bonds that Fendler owned, supplemental cash soon came from a botanical source. William Marriott Canby, a wealthy railroad owner at Wilmington, Delaware, and collaborator of many botanists including Engelmann and Gray, soon "looked in" on Fendler at the urging of the former. Eventually Canby managed to persuade Fendler to move to Wilmington where the brothers bought a small house and established a fine garden. Canby employed Augustus in preparing and arranging herbarium specimens and enjoyed his conversation about the wonderful and curious vegetation of the tropics.

Meanwhile both Canby and Gray viewed with

growing dismay Fendler's attention to his "Mechanism of the Universe." So concerned was Gray that he wrote Engelmann on 19 June 1874: "I wish he had let Cosmical Science alone! But now he never will and is a gone goose." Gray's own practice of eschewing the metaphysical debates about Darwinism informed this judgment. Canby confirmed that "nothing could persuade him that this book was not to bring him everlasting fame and no reasoning could discourage him from undertaking the expenses of publishing this work" (Canby, 1885). Despite his reservations, Gray assessed Fendler's work in "Cosmical Science" in a more affirmative fashion later: "In the year 1874 he published at Wilmington, Delaware, where he then resided, at his own expense [about $300] and, we suppose, with small returns, a well-written treatise (of 154 pages, 8vo) on 'The Mechanism of the Universe and its primary effort-exerting Powers; the Nature of Forces and the Constitution of Matter, with remarks on the Essence and Attributes of the All-Intelligent.' He was one of the ingenious race of paradoxers, and it may be left to the future De Morgan to characterize his work. He will certainly be lastingly and well remembered in botany" (Gray, 1884). Fendler was pleased enough that Joseph Henry bought a copy of the book.

On 15 April 1875 he told Engelmann that Gray had visited him and Charles C. Parry, too. Parry had cut his teeth as a collector in the Mexican Boundary Survey and was about to join Edward Palmer at San Luis Potosi in Mexico. Fendler hadn't seen Gray in ten years. Although he was glad to learn that Gray was now steadily churning out parts of the *Synoptical flora of North America,* he was surprised at how he had aged. This prompted some assessment of his own and Engelmann's situation (9 November 1875):

> Even though Gray told me during our meeting last spring, that I still look as I did ten years ago, I feel the coming on of old age since next January I shall have completed my 63rd year. I believe you are five years older than I and Gray three years, Parry ten and Canby fifteen younger.
>
> [And elsewhere:] You ask whether I am now satisfied with my life. It seems to be a natural trait in a human being who has moved around so much and so constantly, that he wishes to have a quiet home at least in his old age where he can spend the last days of his life without worries. I believe I have reached this aim. Whatever I was looking for, I found. In the winter I am busy with literary works I like, in the summer plant collecting and I find much satisfaction and pleasure. Some times I have the desire, as in younger years, to go far into the woods and meadows and to read the '1000 flowers' which the earth offers in such abundance even in the most distant lands. Especially, I should like to see again the jungle of the tropical mountain areas where I once wandered and look up the old and well known vegetation in all its hiding places. But physical weakness from which I sometimes suffer, reminds me to stay quiet at home. However, I had given some serious thoughts to find enough subscribers to Venezuelan ferns to support such an enterprise financially. The Sea of Valencia with its beautiful and pleasant natural scenery, its picturesque surrounding hills and its incomparable lovely climate is very tempting to me and I should like to enjoy again the balsamic evening and morning air. However, I would only decide to take such a trip if the rheumatism which attacks me regularly during the winters in Delaware continues and makes my life miserable.

The next spring Fendler observed flowering and leaf vernation in oaks for Engelmann (Fendler to Engelmann, 16 May 1876); the two compared meteorological information over the next few years as well. Finally, however, the rheumatism that had plagued Fendler in recent years increased his discomfort so much that he decided to move to Trinidad where he hoped to both find relief and continue contributing to botany and meteorology in his final years. Engelmann asked him to pay close attention to the cacti there to which Fendler replied (6 May 1877):

> In his *Flora of the British West Indian Islands,* Grisebach only described one single species of Cactaceae growing in Trinidad, namely *Rhipsalis Cassytha.* From all the British West Indian Islands, he had of Mamillaria 1, Melocactus 1, Cereus 7, Rhipsalis 2, Opuntia 5, Peiriscia [=Pereskia?] 1, all in all only 17 species. I very much doubt that this is the complete number.

Once in Trinidad Fendler wasted no time and sent Gray fifty sets of about seventy-five species each of ferns, which Gray described as "nice and

satisfactory." Unfortunately, Fendler had no luck in finding cacti. However, he happily reported to Engelmann (26 August 1878) that he had "125 species [of ferns] in my own collection and intend to get up to 200 . . . [and] Euphorbiaceae are strongly represented [here]." Even in the 1870s tropical forests were being ravaged by progress, and Fendler lamented: "Here in Trinidad, a small railroad is being built (the second one); it is a pity that I did not learn about this earlier so that I could have been present at the cutting down of the trees." Despite this and his general disgust with the "folly and rancor of the surging multitude" both in Trinidad and in Delaware (an event that reinforced this shortly before he left Wilmington will be recounted momentarily), Fendler still felt that his final days just might be a little idyllic. "The time for the mangos and breadfruit has almost past," he wrote in August, "but the branches of the two orange trees are bending down already under the burden of their fruit which will not be ripe until October." He later reported (6 January 1881) that he and his brother customarily ate 5 to 6 oranges daily (over 1200 oranges from their trees in six months), numerous plantains and pure chocolate that they prepared themselves from the cocoa beans they grew.

Shortly before Fendler had left Delaware the police had been alerted by some ignorant people who, presumably unaware of the profession of plant collecting, suspected the Fendlers of counterfeiting money. Consequently, the over-zealous officers searched the house and even dug up the garden in search of contraband. Finding nothing they, nevertheless, left everything a mess. After arriving in Trinidad, Fendler wrote Canby: "That this little affair weighed heavily upon my mind and gnawed deep into my immoderately sensitive feelings, you may well imagine."

On 26 March 1879 Fendler's compassionate heart went out to his bereaved friend in St. Louis who had informed Augustus in his 27 February letter of the death of his wife. Fendler could only:

> hope that the hand of your son will heal better than you think and also that your health will be improved in the meantime, so that you can still count on a long and fruitful life. It must be a comfort to you that you are surrounded by many admirers and friends and that you enjoy all the comforts a human being craves.

Engelmann, in his turn, counseled his friend that he was too sensitive, nervous and easily upset. Fendler responded (6 September 1879):

> Why I am concerned with the rabble which surrounds me constantly and which only reminds me too vividly of the degradation of the human race into animals or the opposite, from an animal to a human being [I do not know], but the disgusting impressions remain the same. Fortunately, the masses have not much to say in this country.
>
> [Other things also occupied his mind, however.] For the last 35 years since we became friends, I never lost track of your successful career. That your usual good health is becoming worse is probably due to the late sad events and I hope that you will be well again soon . . . . From the New York Tribune I see what tremendous progress the 'far west' especially Colorado is making lately, especially with regard to population and wealth. If one thinks back of the times and conditions of the regions of the territories west of the Mississippi when we came to St. Louis, I in 1838 and you even earlier, it seems that the developments made during the last years are as wonderful as the tales from '1000 and one night[s]'. But how will things look in the United States after another 40 years?

In 1881 Engelmann traveled to the "far west" and reported to Fendler his observations on his trip from San Francisco to Vancouver on a steamer. In the meantime Fendler kept collecting and also occupied himself with weather data. He helped Henry Prestoe, Superintendent of the Port-of-Spain Botanic Gardens (1864–1886), "figure out the average numbers of his fourteen years of meteorological observations" and sometimes worked for him as a clerk, that "spirit-killing" occupation. Fendler was glad to hear from Engelmann that George W. Letterman had "become such an eager and energetic collector and observer, especially, since, as you say, I gave him the first push" (Fendler to Engelmann, 6 July 1881). But when Engelmann informed him that F. J. Lindheimer, the long-time collector that Fendler had met in Houston in 1839, had died in 1879, Fendler was reminded once more of his own frail condition. Augustus even may have suffered a mild heart attack "lifting a wooden fence" that he and his brother "tried to put into the right place." He described it thus:

> I injured myself (apparently my chest and

> back) and then immediately suffered from an attack of rheumatism, from which I have not yet recovered. The pains in the chest are a great nuisance sometimes, especially if they occur around the heart (6 July 1881).

In the same letter he learned that Engelmann's health was not improving either. However, none of this deterred him from exploring Trinidad. He regaled Canby (1885) with an amusing tale of his encounter with a local dealer in what, from all appearances, had to be hallucinogenic drugs:

> Having ascended one of the highest ridges of the Saut d'eau mountains, about ten miles from town, I took occasion to visit a man known all about as Popo Fernand (though his real name is Joseph Isidore), in order to inquire of him about a piece of land that was offered for sale in his neighborhood. On my way thither I was astonished to find that in and beyond the village of Maraval every man, woman and child knew where the man lived, though his cabin was miles away in the mountains in an out-of-the-way place. When I at last reached his premises I found no one there, but noticed, as something unusual, a great number of beehives stuck all around his cabin and outhouses, the first beehives that I have seen in Trinidad. After a while a woman came up and called aloud Fernand's name. He soon made his appearance. Neither he nor any of his neighbors could speak English and I could not speak their language . . . . The man seemed, however, to be courteously disposed. In order to see how the land lay, I exposed my little pocket compass in his presence, when at once he seemed to become alarmed, and made me understand that he thought the instrument was intended to show the spot where money was hid in the ground. Of this notion I tried to disabuse him. Soon after he invited me into his room and, as is customary here . . . he asked me to help myself to the contents of a small bottle he set before me. Not to show any signs of distrust, I poured out about two thimblefuls of the liquor, mixing it with plenty of water, but became somewhat suspicious after drinking it on noticing that Fernand himself had not taken any of the bottle's contents. About ten minutes later, on my way back, I experienced a strange state of mind such as never before I had happened to be in. There were neither dizziness, stupefaction nor exhilarating symptoms. Visions and strange incoherent thoughts flashed across my mind continually and vanished at once as quickly as they came. Any theme I made an effort to think upon slipped from my memory, and instead thereof quite a different theme presented itself with the same futile result, until I became frightened at my own thoughts and terrified at my condition of mind. After a two hours brisk and steady walk this unpleasant irritation of mind gradually subsided . . . . What would have been the result had I taken a little more of that liquor?

In the summer of 1881 Fendler informed Engelmann that he had sent J. D. Hooker five sets of his phanerogams. So Kew also was reaping part of Fendler's harvest. But they had done so before. In fact, years earlier Hooker had written Gray praising Fendler's Santa Fe specimens (Dupree, 1959). Augustus also remarked that Henry Shaw seemed to be one of those long-lived people who might reach his father's age, near ninety. He fondly recalled and inquired about Shaw's sister and brother-in-law. A year later, 20 July 1882, his last letter to Engelmann (that we know of) states:

> I received your letter of May 24th on June 20th and was glad to learn that you did not suffer from rheumatism for quite a while. What I mistakenly thought was rheumatism, when I wrote you my last letter on January 4th, turned out to be a congestion of the liver, a dangerous one, as the doctor told me; after taking the medicine he prescribed I felt quite well several weeks later.
>
> Lately, however, I don't have much appetite which is probably the result of the continuous heat and humidity, I also suffer from a weakness in all bones and especially the back. I believe, too, that a higher area would be better for my health, about 4000 to 5000 feet above sea level. I also should like to visit Colonia Tovar again and collect ferns there and am waiting for a reply to my letters to several gentlemen with regard to the sale of these, and also to learn something about the present condition of the colony. It was destroyed several years after I left there; I have not yet been able to find out whether it was rebuilt again. [He provided some weather data, promised him a specimen of

Mamillaria papyracantha, and observed that] we expect to have streetcars in Port of Spain which will be a great convenience for me.

Fendler may have enjoyed the trolleys for a short time, but he never returned to Colonia Tovar nor did he ever find his utopian farm in the backlands of Trinidad. Death struck him down on 27 November 1883. His life-long friend Engelmann had a memorandum of this event (how recently arrived is not known) on his desk at the time that he died, namely 4 February 1884; Fendler was 71, Engelmann 76 (Gray, 1885).

Canby had written in 1885 that only "brief notices" about Augustus Fendler had appeared in scientific periodicals since his death, "but scarcely such as so excellent a man and one so useful to science deserved." Perhaps these selections from his letters to Engelmann will lengthen the deserved notices about this man so beloved of Canby, Gray and Engelmann. (For the most recent bibliography on Fendler's life and works, see Stafleu and Cowan, 1976, vol. 1, pp. 822, 823, 990).

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THE EVER-CHANGING LANDSCAPE OF CACTUS SYSTEMATICS[1]

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ABSTRACT

Since Linnaeus originally described 22 species in the single genus *Cactus,* over 11,000 binomials and 400 generic names have been proposed for Cactaceae, and the nomenclature of cacti has been in a constant state of change and turmoil. When Engelmann began his cactus studies, only 25 generic names had been proposed, and the family was not well collected. Engelmann described and skillfully illustrated many cacti from the western United States and northernmost Mexico. By 1900, all known columnar species were classified in *Cereus* Miller; but soon Britton and Rose subdivided this form genus into many smaller and more homogeneous units. The descriptive phase of cactology has slowed, and since Buxbaum researchers have attempted to unravel the evolution of the family and to express phylogenetic information in a generic classification. One area of active phylogenetic research has been in tribe Pachycereeae, which includes the large columnar cacti of Mexico and adjacent areas. These species are often treated as two subtribes: Stenocereinae, which includes species with funicular pigment cells, abundant stem triterpenes, and seeds with verrucose testa having prominent striae; and Pachycereinae, which includes species that lack funicular pigment cells and that often have stem alkaloids but no triterpenes and seeds with smooth testa. New chemical surveys of Stenocereinae have revealed that an individual stem usually has a great number of triterpene glycosides and flavonoids. Crude visual comparisons are made of chromatographic patterns in triterpenes and flavonoids to evaluate existing phylogenetic hypotheses of the species groups. New reports of alkaloids in Pachycereinae are presented for *Lemaireocereus hollianus, Neobuxbaumia mezcalaensis, Pachycereus grandis,* and several species of *Cephalocereus,* but alkaloids are definitely absent in some of the species of *Cephalocereus* and *Neobuxbaumia* as well as *Mitrocereus.* In addition, alkaloids are reported here for the first time in species of Stenocereinae.

Cacti are famous for their beautiful flowers and many bizarre vegetative features, but they are equally famous—or infamous—for their nomenclatural and systematic problems, which are, indeed, formidable. Although most botanists are overwhelmed or greatly confused by the taxonomic literature on Cactaceae, some strides have been made to unravel the phylogeny of this family, which includes about 120 genera and 1,550 species (Gibson & Nobel, 1986). Moreover, systematic goals for cacti are no different than those met and addressed in any large and diverse family of plants: 1) to define the limits of each species; 2) to choose the oldest valid binomial; 3) to recognize monophyletic taxa; 4) to define the criteria to be used for erecting each genus; and 5) to produce a truly phylogenetic classification of the genera. This paper examines the problems of producing a phylogenetic classification for cactus genera. Following a brief review on the remarkable taxonomic legacy of Cactaceae, discussions will concentrate on the columnar cacti of tribe Pachycereeae to demonstrate what types of research are needed to solve systematic problems in this family.

A BRIEF HISTORY OF CACTUS TAXONOMY

Christopher Columbus and his crew were undoubtedly the first Europeans to see cacti (Howard & Touw, 1981). Unfortunately, cacti were not mentioned in the published logs of the Columbus voyages (Morison, 1963), so this statement cannot be verified; but these explorers could not have missed cacti, which constitute a conspicuous part of the vegetation in the West Indies. Apparently the earliest New World description of cacti by a European was contributed by Oviedo (1526), who lived in the New World. Later Hernández (1514–1578) discussed 15 species of cacti in his famous account of Mexican plants that was eventually published in 1615.

By the 17th century cacti were already being cultivated in western Europe. Two unvalidated

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cactus names, "Cereus Peruanus" and "Ficus Indica," appeared on a list of British plants by Gerard (1599). The earliest authentic report of *Melocactus communis* Link & Otto has been credited to Clusius in Holland, who in 1605 was brought a cultivated specimen from the island of Maio in the Cape Verde Islands near West Africa, where it was first spotted by Dutch seamen in 1601 (Heniger, 1973). How *Melocactus,* a New World genus, became established on Maio is a matter of speculation, but the Dutch were probably the ones who introduced this cactus from Curaçao, presumably in the mid or late 1500s. Bauhin and Cherler (1619; Bauhin, 1623; Rowley, 1976) mentioned the presence of species of "Cereus" and "Ficus Indica" in European gardens. Herbarium vouchers of *Opuntia* from the 1660s occur in the bound herbarium (*Hortus Siccus,* L) of Gaymans, a Leiden pharmacist, who documented the plants in Leiden's Hortus Botanicus, the oldest botanical garden in The Netherlands. Many cactus species, including seven species of cereoids, were described from gardens in The Netherlands by Hermann (1687, 1698), and Boerhaave (1720) showed an engraving of the first flowering specimen (1 August 1691) of "Cereus peruvianus" in the Leiden botanical garden. Whatever role other countries had in introducing cacti to Europe is still unstudied, but certainly Dutch horticulturists were central in promoting the early interest in cactus cultivation, which soon became an avid passion of many gardeners.

The Dutch influence on cactus taxonomy extended, of course, to Linnaeus, who studied plants in The Netherlands. In *Hortus Cliffortianus,* which is a garden catalogue of the estate of Dr. George Clifford near Haarlem, Linnaeus (1737) mentioned 16 species in the genus *Cactus* and one species, which has large leaves, in the genus *Pereskia. Pereskia,* a name borrowed from the botanical illustrator Charles Plumier, honored Nicolas Claude Fabri, seigneur de Peiresc, who was a correspondent friend of Clusius. However, when Linnaeus (1753) published *Species Plantarum,* he classified all cacti in a single genus *Cactus,* with 22 species. Assigned to this taxon were platyopuntias, columnar cacti, epiphytes, barrel cacti, dwarf growth forms, and the leaf-bearing cacti. Subsequently, Miller (1754)[5] recognized three additional genera, *Cereus, Opuntia,* and *Pereskia,* based on the earlier common names, to emphasize some major differences in the cacti that were already known. At present, the species described by Linnaeus and Miller are classified in ten or more genera, belonging to three different subfamilies; since Linnaeus about 11,000 Latin binomials and an additional 400 generic names have been published for cacti. Regrettably, most published cactus binomials are illegitimate, invalid, or incorrect, because present-day cactus systematists recognize only 1,400–1,700 valid species and 70–140 genera. Moreover, in 1930, when *Mammillaria* Haworth was conserved, the name *Cactus* L. was declared a *nomen rejiciendum* because the lectotype of the family, *C. mammillaris* L., became a species of *Mammillaria* (Hunt, 1967; Shaw, 1976; Howard & Touw, 1981). Rejecting *Cactus* enabled taxonomists to resolve many nomenclatural problems and to reduce the ambiguity stemming from the inconsistent definitions and usage of *Cactus* by various authors.

Cacti described before 1820 were mostly species that were collected in the West Indies and along the eastern coastline of North and South America, such as from Brazil, Venezuela, Mexico, Florida, and Virginia. Some of the early discoveries were epiphytes, which were so remarkable in vegetative appearance and diversity that new generic names were proposed for the different forms, e.g., *Hariota* Adanson (1763), *Cassyta* J. Miller (1771), *Rhipsalis* Gaertner (1788), *Epiphyllum* Haworth (1812), *Phyllocactus* Link (1831), and *Lepismium* Pfeiffer (1835).

Taxonomic knowledge of Cactaceae accelerated rapidly when botanical exploration penetrated the arid and semiarid regions of the New World. New genera were proposed for low growth forms of Mexico: *Mammillaria* Haworth (1812), *Echinocactus* Link & Otto (1827), *Ariocarpus* Scheidweiler (1838), *Astrophytum* Lemaire (1839), *Echinofossulocactus* Lawrence (1841), and *Pelecyphora* Ehrenberg (1843). Also, Pfeiffer (1838) proposed *Cephalocereus* as the first segregate genus of *Cereus,* based on the type, *Cactus senilis* Haw., an arborescent, solitary columnar cactus from Hidalgo, Mexico. Low growth forms collected in South America and the West Indies were assigned to other new genera: *Melocactus* Link & Otto (1827), *Echinopsis* Zuccarini (1837), *Discocactus* Pfeiffer (1837), and *Gymnocalycium* Pfeiffer (1845).

George Engelmann entered the field of cactus

[5] Literature citations for all generic names mentioned in the following pages can be found in Hunt (1967).

taxonomy in the 1840s, after his reputation as a botanical taxonomist had already been established. Cactus materials collected in the United States and its territories were generally referred to him. Soule (1970), Mitich (1974), and Benson (1982) have written accounts of Engelmann's contributions to cactology between 1845 and 1878. During these years, Engelmann obtained live plants, herbarium specimens, first-hand descriptions, and illustrations of cacti from western North America and then reorganized, analyzed, and legitimately published names for hundreds of new taxa. Not all of Engelmann's names have survived careful systematic analysis, but it is a tribute to Engelmann that a great many of them are still considered correct.

The vast majority of common cacti of the southwestern United States and adjacent Mexico were first described by Engelmann, including seven of the ten cereoid species of the United States–Mexico borderland, 17 species and three varieties of cylindropuntias, about 20 species and varieties of platyopuntias, and over 50 species of the globular, caespitose, and barrel forms. Half of the binomials and trinomials accepted by Benson (1969a, 1969b, 1982) in the large cactus flora of California and Arizona have Engelmann as an authority, and Wiggins (1980) accepted 24 Engelmann taxa in Baja California, particularly species that occur in the northernmost latitudes. Specific epithets commemorate the people who collected specimens for his studies in St. Louis: *Ferocactus wislizenii* (Engelm.) Britt. & Rose, *Opuntia parryi* Engelm., *O. stanlyi* Engelm., *O. lindheimeri* Engelm., *O. bigelovii* Engelm., *Lophocereus schottii* (Engelm.) Britt. & Rose, *Stenocereus thurberi* (Engelm.) Buxb., *Peniocereus greggii* (Engelm.) Britt. & Rose, *Echinocereus fendleri* Engelm., and *Mammillaria wrightii* Engelm. Each taxon was very carefully described, and many were exquisitely illustrated by Paulus Roetter. Engelmann was also the person who proposed the genus *Echinocereus* (Engelmann, 1848), although he later changed his mind (Engelmann, 1849); and he recognized the distinctiveness of *Coryphantha,* which was later elevated to generic rank by Lemaire (1868).

Lemaire, who studied cacti during the same period as Engelmann, also made many individual contributions to cactus taxonomy for North and South America. He published 12 new generic names, at least six of which are still widely recognized (*Aporocactus, Cleistocactus, Schlumbergera,* and *Tephrocactus,* as well as the two Lemaire genera already mentioned). At that time South American cacti were still relatively unknown, although Philippi (1860) reported new Chilean discoveries and described three distinctive genera, *Eriosyce, Eulychnia,* and *Maihuenia.* Cactus studies in arid and semiarid regions of North America were progressing through the floristic studies of Coulter, Orcutt, the Brandegees, and Weber. Weber also conducted cactus investigations on the Galápagos Archipelago and the epiphytic species of Costa Rica.

The taxonomic history of cacti was directed mostly by large descriptive monographs of the entire family, instead of by smaller monographs of individual genera. The first broad familial monograph was published at the turn of the century by Schumann (1898). Judged by today's standards, this classification is considered primitive, but Schumann made several interesting contributions. He was the first person to divide cacti into three subfamilies, which are still in use: Cereoideae, the largest taxon, which is now properly renamed Cactoideae in accordance with Article 19 of the International Code; Opuntioideae, which are the species having a white, bony aril covering the seed; and Peireskioideae (now spelled Pereskioideae), the large, relatively nonsucculent cacti that have large leaves (*Pereskia*) and the closely related *Maihuenia,* which are cushion plants (Gibson, 1977). Schumann recognized 21 genera, and he grouped the genera of Cactoideae into three tribes, Echinocacteae (including the cereoids), Mamillarieae, and Rhipsalideae. These divisions were not phylogenetic in any modern sense. He rejected the name *Cactus* before it was proper to do so, and for the low growth forms he accepted many of the valid segregate genera that were mentioned above. Schumann ultimately proposed four new genera, *Zygocactus* (1890), *Rebutia* (1895), *Pterocactus* (1897), and *Wittia* (1903), but oddly enough he did not use either *Zygocactus* or *Rebutia* in his 1898 monograph; indeed, he did not even recognize *Rebutia* as a subgenus of *Echinocactus,* and he made *Zygocactus* a synonym of *Epiphyllum* Haw., which he and other cactologists totally misunderstood.

In 1904 Britton and Rose began their famous studies on the taxonomy of Cactaceae, which included a careful reexamination of all original descriptions and type specimens, extensive new field work in cactus areas throughout the New World, and assemblage of large living and dried collections for close study and photographing. Beginning in 1911, these studies were financed

by the Carnegie Institute of Washington, and Britton and Rose (1919–1923) eventually produced a four-volume taxonomic monograph, *The Cactaceae,* which is familiar to every systematic botanist and cactologist and is undoubtedly the most commonly cited and central cactus reference.

To discuss the contributions of Britton and Rose, some attention first must be paid to Berger, who was curator of the botanical gardens in La Mortola, Ventimiglia, Italy. Berger (1905) published a revision of the genus *Cereus* in which he recognized 18 subgenera. Many of these names were later used as genera by Britton and Rose but often in a much modified form. In Berger's revision, the columnar cacti that were known to him were those species that occurred in Mexico, the West Indies, Costa Rica, Peru, Chile, Argentina, and Brazil.

To assess fully the taxonomic contributions of Britton and Rose would take a very long article, half of which would consider the progressive, positive changes initiated by them, and half would analyze the errors in determination and judgment. Clearly, this familial monograph was and still is the cornerstone of cactus systematics. Britton and Rose accepted Schumann's three subdivisions, although they renamed these as tribes. In a massive revision of subfamily Cactoideae (Tribe Cereeae), Britton and Rose recognized 114 genera in eight subtribes and subdivided *Cereus* into many smaller and more homogeneous units. With this action, species of columnar cacti were placed into seven of the eight subtribes, and the name *Cereus* became restricted in usage to a small group of species in eastern and southern South America. Britton and Rose together described 77 new genera, and they published two more genera independently, *Harrisia* Britt. and *Escontria* Rose.

Looking at this great cactus monograph with 20–20 hindsight, it is easy to find many faults. One unfortunate choice was substituting *Neomammillaria* Britt. & Rose for *Mammillaria* Haw., which in 1930 was accepted internationally as a conserved name; this resulted in 186 unnecessary binomials under the new and ultimately illegitimate name. There were, of course, a number of genera that had improper membership, and binomials listed in synonymy have sometimes turned out to be "good" species that belonged in another genera. Moreover, at least 10 genera in the monograph appear now to be too narrowly defined to recognize, especially some names that were proposed as segregates of *Mammillaria* and *Rhipsalis*. Regardless of this, at least 56 generic names of Britton and Rose (out of a total of 79) are widely regarded as sound taxa, although, as we shall discuss, some of these have been greatly redefined or are now being considered as subgenera. Consequently, the generic concept in cactus systematics often corresponds fairly closely to that presented by Britton and Rose.

Berger (1926) published an interesting book on the evolution of cactus genera, in which he used the Britton and Rose classification. Berger (1929) soon after published his own familial monograph, in which he accepted only 41 genera. He used 54 names authored by Britton and Rose but reduced these to subgeneric status. Overall, the classification scheme resembled that of Schumann, having three subfamilies, but in Cactoideae (as Cereoideae) he recognized only two tribes: Rhipsalideae, in which he included the rhipsaloid epiphytes plus *Epiphyllum*; and Cereeae, with four subtribes, in which he placed all other species of the subfamily. Consequently, the subtribal classification of Berger differed markedly from that of Britton and Rose.

Berger's 1929 classification system had many unusual and inconsistent features. For example, in "subsubtribus Echinocacteinae" the genus *Echinocactus* was very broadly defined, much like *Cereus,* and included barrel and small cacti from North and South America. However, in this subsubtribe he also included five monotypic Mexican genera, *Lophophora, Aztekium, Obregonia, Epithelantha,* and *Leuchtenbergia,* that are no less distinctive than some of the subgenera that he retained in *Echinocactus.* Likewise, in his subtribe Mamillarieae, Berger recognized 10 genera, of which six are no longer recognized; and in tribe Rhipsalideae he recognized six genera and many subgenera, most of which are not accepted now. Consequently, in this "conservative" classification, 13–15 of the 41 genera were more narrowly defined that most current cactus systematists would accept.

Cactologists universally acknowledged the great contribution of Britton and Rose, who were trained taxonomists. Bravo (1931, 1937) followed Britton and Rose in studies of the Mexican cacti, which are still being updated (Bravo, 1979); consequently, many collectors studying Mexican cacti have also followed Britton and Rose. Nonetheless, Schelle (1926) published a classification scheme that followed Berger (1905).

Working with a different generic concept were Frič, Backeberg, Ito, and other cactus horticulturists, who published many new generic names, more narrowly defined and often based on minor features. This new wave of classifications was stimulated first by the discoveries of new and exciting cacti in South America. Botanists and cactus growers began to collect extensively in the rich cactus areas of western South America. The plants that arrived in Europe from Ecuador, Bolivia, Peru, Chile, Uruguay, and Paraguay greatly changed the data base used by Britton and Rose to evaluate the South American genera.

The greatest source of new generic names was Backeberg. Slowly at first and then with a flourish, Backeberg (1958–1962, 1966) proposed many new genera and hundreds of species and varieties for South American materials. At the same time, he greatly subdivided and redistributed most of the Britton and Rose genera from the rest of the New World. In all about 81 generic names were published by Backeberg; however, today only 15–20 of these are still being considered seriously in taxonomic circles as useful taxa for a phylogenetic classification.

Backeberg was just one of several cactus horticulturists who increased the generic confusion of Cactaceae. For example, Frič published 52 new generic names, but of these only *Obregonia* has survived (Anderson & Skillman, 1984); and Ito proposed 18 new names, of which none have been widely accepted. Backeberg, Frič, Ito, and many other cactus enthusiasts were fascinated by variability of cacti, so they emphasized fairly minor and often plastic features in erecting new varieties, species, and genera. To be sure, commercial cactus businesses generally favored very liberal nomenclature to emphasize differences between plants. Nonetheless, there has been a backlash by numerous cactologists, both professional botanists and serious collectors, who have worked hard over the last 20 years to curb indiscriminate overnaming. Space limitations here do not permit a full review of the studies—published over the last 20 years—in which the number of species and genera has been carefully reevaluated.

In North America the most remarkable part of this narrative unfolded. Cactus enthusiasts generally adopted Britton and Rose and began in earnest to define the species and varieties and to produce monophyletic genera. In contrast, Benson (1940) set out to study the cacti of the United States and Canada using the careful techniques of Engelmann but the generic concept of Berger. Hence, in all cactus floras published by Benson (1969a, 1969b, 1970, 1982) and in floras and ecological studies that relied on Benson's monographs, such as the flora of Texas (Correll & Johnston, 1970), columnar cacti were classified in *Cereus* s.l. Benson (1969a) has briefly defended his reasons for using *Cereus*. From his viewpoint, "there is no 'right' or 'wrong' system" (p. 8), and a system should be one that conforms with the classification systems of other taxa and that is 'practical.' Benson felt that a conservative policy, i.e., placing all columnar forms in one genus *Cereus,* was in harmony with the overall conservative policy of plant systematics, and he also labeled the efforts of Britton and Rose as part of a "local 'liberalism'" that prevailed in the United States. He also felt that there are so few columnar cacti north of Mexico that it would be impractical to recognize so many monotypic genera for this area.

No other cactus taxonomist in recent history has agreed with Benson about the classification of columnar cacti. The reasons for this are many, but only two major points need to be discussed. First, the diversity of vegetative and reproductive features in columnar cacti is as great as the diversity of features present in low growth forms of North America, which Benson has recognized as distinct genera. Second, in order to understand and describe the phylogeny of the low growth forms in Cactoideae, which originated from columnar taxa, it is imperative to determine which part of the cereoid complex is the putative ancestor or sister taxon. The goal of modern cactus systematics, like that of the rest of plant systematics, is to make certain that each taxon above the species level is monophyletic in the strictest sense and reflects phylogeny.

Because none of the currently used classification systems for Cactaceae has been able to show that all taxa used are monophyletic, botanists can expect one more period in the history of cactus systematics in which traditional systems are studied intensively and rewritten to fit the modern guidelines for presenting phylogenetic hypotheses.

PACHYCEREEAE: AN EXAMPLE OF TAXONOMIC COMPLEXITIES

The Austrian botanist Franz Buxbaum deserves full credit for initiating a movement to develop a truly phylogenetic system of classifi-

cation for Cactaceae. He published many morphological papers on cacti (for a partial listing, see Gibson & Horak, 1978) during the same period that Backeberg was publishing his long list of segregate genera. The timing was unfortunate, because, in general, plant systematists were greatly distressed by the deluge of generic cactus names and paid little attention to new cactus publications, including the phylogenetic studies of Buxbaum. Although Buxbaum accepted a number of Backeberg names, he also studied the relationships of the species and provided excellent observations for rejecting many of Backeberg's conclusions.

Although Berger (1926) published on the generic relationships within Cactoideae, actually it was Buxbaum (1958) who proposed the first innovative phylogenetic classification of cactus genera and therein proposed most of the contemporary tribal names. Of these, Pachycereeae is the tribe that includes the large columnar cacti of Mexico and several other species that occur outside Mexico in the West Indies, Central America, and northern South America (Gibson & Horak, 1978; Bravo, 1979; Gibson, 1982). Buxbaum defined this tribe chiefly by listing the genera that he included in it. No synapomorphy currently defines this tribe in a strict cladistic sense; consequently, no one can categorically state which genera and species must be included. In the narrowest definition of the tribe, about 70 species would be included; there may be species in South and Central America that might be included but presently are not classified in this tribe. One derived feature that occurs in all species so far included is a wood skeleton composed of a ring of parallel, discrete, fastigiate rods (Gibson, 1978). A few columnar cacti in northern South America, e.g., *Neoraimondia,* have this design but are currently classified in tribe Leptocereeae Buxb.

Tribe Pachycereeae can be effectively used as a model to show the systematic complexities of Cactaceae. Coincidentally, some of the species were first described by Engelmann, and even in his time there was a debate on generic names for columnar forms. In fact, numerous species of Pachycereeae have been transferred between genera, and a few have valid binomials in four or more genera. Another advantage of studying this tribe is that the alpha taxonomy of the Mexican species has been done (Bravo, 1979). To complement this, much structural and phytochemical data have been collected on these species—more than in any other cactus tribe—which has enabled workers to attempt phylogenetic reconstructions using contemporary methods. Finally, phylogenetic modeling of this tribe is now in a new, third generation, so that older phylogenetic models can be tested to determine whether the original criteria still yield a parsimonious solution.

The taxonomic history of Pachycereeae began in 1753, when two West Indian species (*Cephalocereus* s.l.) were named by Linnaeus; however, the descriptions of columnar cacti from Mexico did not begin until the 19th century and then continued at a fairly steady pace until 1973, when *Stenocereus fricii* Sánchez Mejorada was described. Columnar cacti were initially described as species of *Cereus* or *Cactus,* but new combinations appeared when three segregate genera were proposed, *Cephalocereus* Pfeiff., *Cephalophorus* Lem., and *Pilocereus* Lem., which all cited the same type, *Cactus senilis* Haw. These segregates described what are broadly referred to as cephalocerei, fruticose and arborescent columnar cacti that have spineless flowers and fruits, relatively few bracts on the ovary and floral tube, and persistent and long, usually white hairs on the floriferous areoles.

The first species of Pachycereeae described by Engelmann was saguaro, *Cereus giganteus* (1848), and this was followed by organ pipe cactus, *Cereus thurberi* (1854), and senita, *Cereus schottii* (1856). In 1856 Engelmann described the subgenera *Lepidocereus, Eucereus, Pilocereus,* and *Echinocereus.* In subgenus *Lepidocereus* he included *C. giganteus* and *C. thurberi* of the Sonoran Desert along with *C. chilensis* Pfeiff. from South America. Subgenus *Pilocereus* included the cephalocerei; *Echinocereus* included the low, caespitose hedgehog cacti of North America; and *Eucereus* included other columnar forms. Two other species of columnar cacti from Mexico, *C. pecten-aboriginum* Engelm. and *C. gummosus* Engelm., were defined by Engelmann but were not published until after his death.

Lemaire recognized *Pilocereus,* in which he eventually placed all known cephalocerei as well as *C. schottii* and *C. giganteus. Pilocereus* was also accepted as a genus by Salm-Dyck, Weber, Rümpler, and Console, and it was used widely in horticultural circles. At the end of the century, Console proposed *Myrtillocactus* (1897) for *Cereus geometrizans* Mart., a distinctive, wide-ranging, arborescent cactus that produces two or more small, spineless flowers per areole. How-

TABLE 1. Classification of Pachycereeae into subgenera according to Berger (1905). Descriptions were abstracted from the key and diagnoses. After each species are listed the names used by Britton and Rose (1920) and Gibson and Horak (1978).

Cephalocereus (Pfeiff.) A. Berg. Flowers produced in a distinct cephalium; ribs with isolated mammillae that are surrounded by long hairs and spines; flowers small and arising singly from each mammilla.		
Cereus chrysomallus Hemsl.	*Pachycereus chrysomallus* (Lem.) Britt. & Rose	?*Backebergia militaris* (Audot) Bravo ex Sánchez Mejorada
C. columna-trajani Karw.	*Pachycereus columna-trajani* (Karw.) Britt. & Rose	*Cephalocereus hoppenstedtii* (Weber) K. Schum.
C. macrocephalus (Weber) A. Berg.	*Cephalocereus macrocephalus* (Haw.) Britt. & Rose	*Neobuxbaumia macrocephala* (Haw.) Buxb.
C. melocactus (Vell.) A. Berg.	*Cephalocereus fluminensis* (Miq.) Britt. & Rose	Unassigned
C. senilis DC.	*Cephalocereus senilis* (DC.) Pfeiff.	*Cephalocereus senilis*
Lophocereus A. Berg. Flowers several from each areole; flowering areoles differing from vegetative areoles by having numerous long setulose bristles; flowers reddish or yellowish; fruits scaly.		
Cereus schottii Engelm.	*Lophocereus schottii* (Engelm.) Britt. & Rose	*Lophocereus schottii*
?*C. scoparius* (Poselg.) A. Berg.	*Cephalocereus scoparius* (Poselg.) Britt. & Rose	*Neobuxbaumia scoparia* (Poselg.) Backeb.
?*C. urbanianus* (K. Schum.) A. Berg.	*Selenicereus urbanianus* (Gürke & Weing.) Britt. & Rose	Tribe Hylocereeae
Myrtillocactus (Cons.) A. Berg. Flowers very small, several per areole; ovary naked with a few minute scales; fruits small, smooth, reddish brown berries.		
Cereus geometrizans (Mart.) Cons.	*Myrtillocactus geometrizans* (Mart. in Pfeiff.) Cons.	*Myrtillocactus geometrizans*
Pachycereus A. Berg. Flowers solitary, actinomorphic, tubular; ovary and tube covered with dense hair and thin bristles.		
Cereus pringlei S. Wats.	*Pachycereus pringlei* (S. Wats.) Britt. & Rose	*Pachycereus pringlei*
C. pecten-aboriginum Engelm.	*Pachycereus pecten-aboriginum* (Engelm. in S. Wats.) Britt. & Rose	*Pachycereus pecten-aboriginum*
C. thurberi Engelm.	*Lemaireocereus thurberi* (Engelm.) Britt. & Rose	*Stenocereus thurberi* (Engelm.) Buxb.
C. fulviceps (Weber) A. Berg.	*Pachycereus chrysomallus* (Lem.) Britt. & Rose	*Mitrocereus fulviceps* (Weber) Backeb. ex Bravo
C. orcuttii K. Brandeg.	*Pachycereus orcuttii* (K. Brandeg.) Britt. & Rose	× *Pachgerocereus orcuttii* (K. Brandeg.) Moran
Lepidocereus (Englem.) A. Berg. Flowers solitary, actinomorphic, tubular, and large; greenish white; ovary with little short wool and sometimes a few deciduous bristles; fruits obovoid or pear-shaped with small and remote deltoid scales; plants very tall.		
C. giganteus Engelm.	*Carnegiea gigantea* (Engelm.) Britt. & Rose	*Carnegiea gigantea*
Stenocereus A. Berg. Flowers solitary, actinomorphic, tubular, small, and reddish or brown; ovary globose and with deltoid scales, naked, or with a few setulose hairs and little wool; fruit globose, brownish, and with a reddish pulp.		
Cereus chiotilla Weber	*Escontria chiotilla* (Weber) Rose	*Escontria chiotilla*
C. dumortieri Salm-Dyck	*Lemaireocereus dumortieri* (Scheidw.) Britt. & Rose	*Stenocereus dumortieri* (Scheidw.) Buxb.
?*C. marginatus* DC.	*Pachycereus marginatus* (DC.) Britt. & Rose	*Pachycereus marginatus*
C. sonorensis Rünge	*Rathbunia alamosensis* (Coult.) Britt. & Rose	*Stenocereus alamosensis* (Coult.) Gibson & Horak

TABLE 1. Continued.

C. stellatus Pfeiff.	*Lemaireocereus stellatus* (Pfeiff.) Britt. & Rose	*Stenocereus stellatus* (Pfeiff.) Riccob.
C. alamosensis Coult. (juvenile form of *C. stellatus*)	*Rathbunia alamosensis*	*Stenocereus alamosensis*
C. aragonii Weber	*Lemaireocereus aragonii* (Weber) Britt. & Rose	Unassigned
?*C. pruinosus* Otto	*Lemaireocereus pruinosus* (Otto) Britt. & Rose	*Stenocereus pruinosus* (Otto) Buxb.
?*C. eburneus* Salm-Dyck	*Lemaireocereus griseus* (Haw.) Britt. & Rose	*Stenocereus griseus* (Haw.) Buxb.
?*C. resupinatus* Salm-Dyck	*Lemaireocereus griseus*	*Stenocereus griseus*
?*Pilocereus tetetzo* Weber	*Cephalocereus*?	*Neobuxbaumia tetetzo* (Weber) Backeb.
Pilocereus A. Berg. Flowers campanulate; ovary with very few scales and naked; fruit smooth and naked.		
Cereus chrysacanthus (Weber) A. Berg.	*Cephalocereus chrysacanthus* (Weber) Britt. & Rose	*Cephalocereus chrysacanthus*
C. exerens Link	*Cephalocereus arrabidae* (Lem.) Britt. & Rose	Unassigned
C. hermentianus Monv.	*Cephalocereus hermanentianus* (Monv.) Britt. & Rose	Unassigned
C. hoppenstedtii (Weber) A. Berg.	*Cephalocereus hoppenstedtii* (Weber) K. Schum.	*Cephalocereus hoppenstedtii*
C. houlletii (Lem.) A. Berg.	*Cephalocereus leucocephalus* (Poselg.) Britt. & Rose	*Cephalocereus leucocephalus*
C. lanuginosus Mill.	*Cephalocereus lanuginosus* L.	Unassigned
C. royeni L.	*Cephalocereus royenii* (L.) Britt. & Rose	*Cephalocereus royenii*
C. strictus P. DC.	*Cephalocereus nobilis* (Haw.) Britt. & Rose	*Cephalocereus nobilis*
C. ulei (K. Schum.) A. Berg.	*Cephalocereus ulei* Gürke	Unassigned
Eucereus (Engelm.) A. Berg. Flowers large with a long and slender tube; ovary with numerous small deltoid scales; fruit more or less roundish and reddish, covered with spines that are often deciduous in clusters.		
Subsection *Nyctocereus*. Flowers nocturnal; stems more or less upright, cylindrical, and ribbed.		
Cereus bavosus Weber	*Lemaireocereus hollianus* (Weber) Britt. & Rose	*Pachycereus hollianus* (Weber) Buxb.
C. candelabrum Weber	*Lemaireocereus weberi* (Coult.) Britt. & Rose	*Pachycereus weberi* (Coult.) Backeb.
C. cumengei Weber	*Machaerocereus gummosus* (Engelm.) Britt. & Rose	*Stenocereus gummosus* (Engelm.) Gibson & Horak
C. eruca Brandeg.	*Machaerocereus eruca* (Brandeg.) Britt. & Rose	*Stenocereus eruca* (Brandeg.) Gibson & Horak
C. gummosus Engelm.	*Machaerocereus gummosus*	*Stenocereus gummosus*
C. queretaroensis Weber	*Lemaireocereus queretaroensis* (Weber) Saff.	*Stenocereus queretaroensis* (Weber) Buxb.

ever, according to Berger (1905), the segregate genera *Myrtillocactus* and *Pilocereus* were not accepted by professional botanists.

Table 1 shows how Berger (1905) classified into subgenera the species of Pachycereeae known to him. Although Berger deserves credit for having the insight to search for subdivisions of the columnar cacti, it is easy to demonstrate now that his subgenera were often artificial. In subgenus *Cephalocereus*, Berger included five species

having "cephalia," four of which actually have pseudocephalia and which now belong to different genera. *Lophocereus* was created for *C. schottii* from the Sonoran Desert, which has multiple flowers from an areole that also produces long bristles, but included here by Berger was an unrelated species from Veracruz, Mexico, and another from the West Indies that is presently classified in tribe Hylocereeae. *Myrtillocactus* sensu Console was accepted as a subgenus, but Berger did not accept or discuss the taxon *C. cochal* Orcutt (1889) from Baja California. *Pachycereus* included species with dense wool and golden bristles on the fruit, but this subgenus also included *C. thurberi* Engelm., which does not fit the description of the subgenus. *Stenocereus* was Berger's most interesting taxon and included many species that are closely related, but the diagnosis of this subgenus was inaccurate. For example, the flowers of *Stenocereus pruinosus* are not small, but rather are 9 cm or more in length; moreover, the flowers of *Escontria chiotilla* have bright yellow petals, not reddish or brown, and the pulp of its fruit is purplish, not reddish. In addition, fruits of *Lemaireocereus aragonii* have a white pulp and those of *Stenocereus dumortieri* have a pulp that is essentially colorless. *Pilocereus* was used in the same sense as Lemaire's except that the type, *C. senilis,* was excluded and placed in subgenus *Cephalocereus.* Finally, Berger combined species having flowers with nocturnal anthesis in subsection *Nyctocereus* in subgenus *Eucereus.*

After Berger published his 1905 version of *Cereus,* Britton and Rose studied columnar cacti and decided to recognize additional genera for the Mexican pachycereine species. The largest genus accepted was *Cephalocereus,* which they interpreted in the comprehensive sense of Lemaire's *Pilocereus,* i.e., all species with spineless reproductive structures and long hairs on the floriferous areoles. Consequently, this genus included species from South America. *Myrtillocactus* was adopted, and the monotype *Escontria* Rose (1906) was proposed for the only species in Mexico with large, translucent, chartaceous bracts covering the flowers and fruit. The generic name *Carnegiea* was proposed to replace subgenus *Lepidocereus*; this substitution eliminated the need to use the polyphyletic taxon of Engelmann and also permitted Britton and Rose to honor the Carnegie Institute for supporting cactus and desert research.

In a landmark taxonomic paper, Britton and Rose (1909) proposed four more genera. *Lophocereus* was raised to generic rank but was reduced from three species in Berger's system to one, *L. schottii. Pachycereus* became a genus similar to the Berger subgenus and was based on the presence of bristles on the fruit. The name *Lemaireocereus* was proposed to include Mexican species that have fruits and sometimes flowers with spine clusters. Species of *Lemaireocereus* were pulled from several subgenera of Berger (Table 1), especially *Stenocereus* and *Eucereus.* Two species with short, tubular, slightly zygomorphic red flowers were also segregated as the genus *Rathbunia.* Britton and Rose (1919–1923) recognized nine genera because they removed two species from *Lemaireocereus* to create *Machaerocereus, M. gummosus* (Engelm.) Britt. & Rose, and *M. eruca* (Brandeg.) Britt. & Rose from Baja California, which have nocturnal anthesis and heavy central spines.

About one month after Britton and Rose published their first major generic monograph, Riccobono in 1909 made an important contribution when he proposed the name *Stenocereus stellatus* (Pfeiff.) Riccob., which was based on subgenus *Stenocereus* of Berger (1905). *Stenocereus stellatus* was an excellent choice for type because it has all of the important features of the stenocerei.

Since Britton and Rose, over 20 generic names have been proposed for the pachycereine plants. Most of these names were added by Backeberg, and these were often defined so narrowly that most had only one or a few species. Consequently, there existed a great need to determine the phylogenetic relationships of the species so that generic decisions could be solidified.

PHYLOGENETIC STUDIES OF BUXBAUM

When Buxbaum (1958) proposed his first phylogenetic hypothesis for Cactoideae, in tribe Pachycereeae Buxb. he accepted six genera, *Pachycereus* Britt. & Rose, *Lemaireocereus* Britt. & Rose, *Neobuxbaumia* Backeb., *Carnegiea* Britt. & Rose, *Cephalocereus,* and *Mitrocereus* Backeb., with *Escontria* Rose and *Anisocereus* Backeb. listed as "genera incertae sedis." He adopted *Pachycereus, Lemaireocereus,* and *Cephalocereus* of Britton and Rose with some important deletions: *Mitrocereus* was a taxon removed from *Pachycereus* and split into two species; *Neobuxbaumia* consisted of some species that had been scattered throughout *Cephalocereus* by past authors; and *Austrocephalocereus* Backeb. consist-

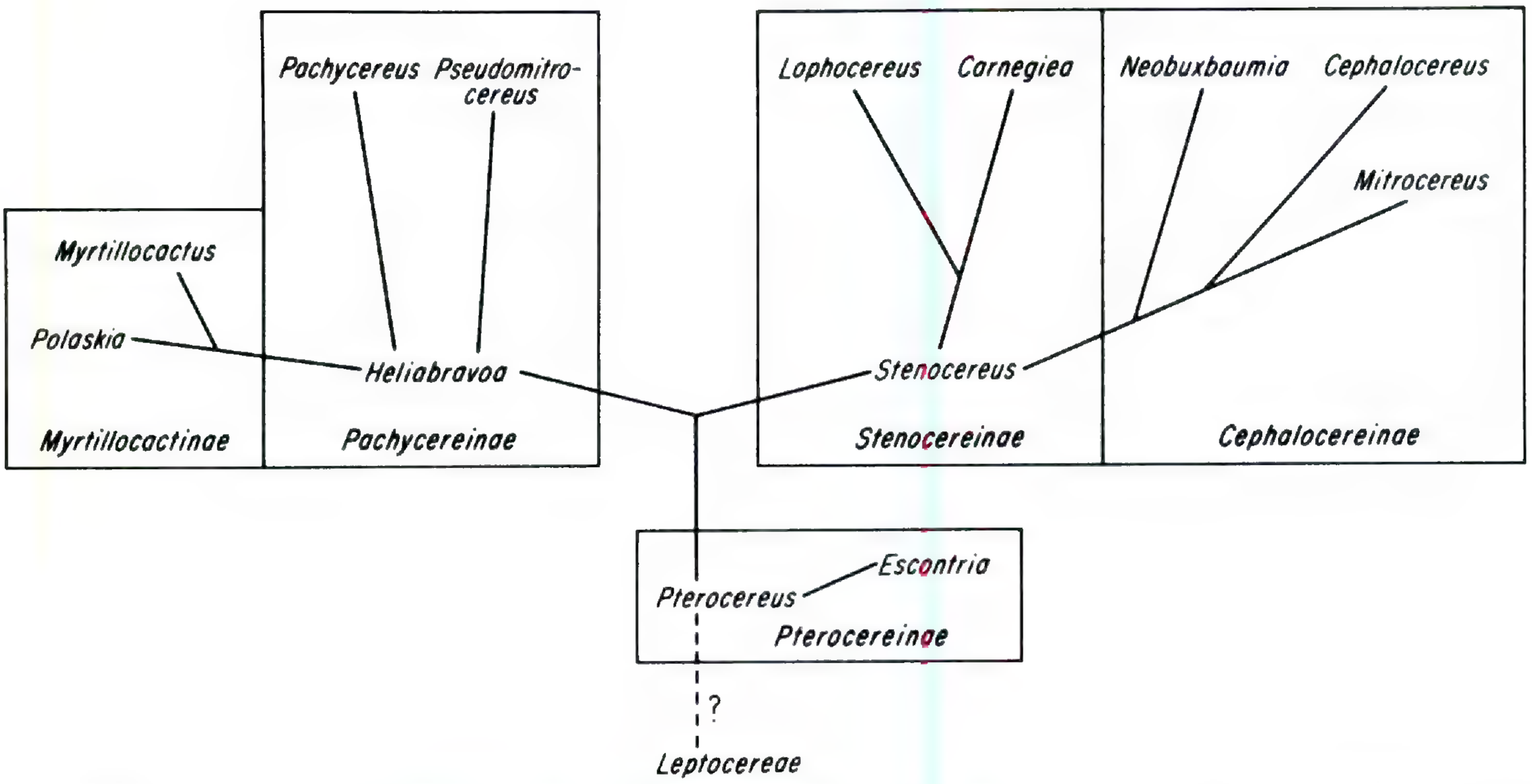


FIGURE 1. The first phylogenetic model of Pachycereeae by Buxbaum (1961), in which he recognized five subtribes and proposed Leptocereeae as the putative ancestor.

ed of South American cephalocerei and was removed to tribe Cereeae Buxb.

Three years later Buxbaum (1961) presented a greatly modified interpretation of Pachycereeae. For its time, this was a remarkably detailed phylogenetic paper on a cactus tribe. Buxbaum recognized 13 genera, and of these only *Neobuxbaumia* and *Carnegiea* were unchanged. *Lemaireocereus* was reduced in size by removal of certain non-Mexican species for reassignment in *Armatocereus* Backeb. of tribe Leptocereeae; by recognition of two monospecific genera, *Heliabravoa* Backeb. and *Polaskia* Backeb., from southern Mexico; and by exchanging several species between *Lemaireocereus* and *Pachycereus* sensu Britton and Rose. At that time *L. hollianus* (Weber) Britt. & Rose, the type, was transferred into *Pachycereus,* which required the adoption of the name *Stenocereus* for the species left in "*Lemaireocereus.*" Three-ribbed species were removed from *Pachycereus* to become the segregate *Pterocereus* Backeb.; and *Anisocereus lepidanthus* (Eichl.) Backeb., which was formerly a species of *Pachycereus,* was added to *Escontria. Mitrocereus,* which originally consisted of two species, was treated as two distinct, monospecific genera, *Mitrocereus* and *Pseudomitrocereus* Bravo & Buxb., which later were renamed *Backebergia* Bravo and *Mitrocereus,* respectively (Sánchez Mejorada, 1973b). In addition, Buxbaum transferred *Lophocereus* Britt. & Rose and *Myrtillocactus* to Pachycereeae from tribe Cereeae. Hence, this tribe began to be redefined as a Mexican taxon with some outliers in the neighboring countries and the West Indies.

Buxbaum described and illustrated the flowers, fruits, seeds, and seedlings more carefully than most previous workers, and he discovered some features that were exceedingly important in analyzing their phylogenetic relationships. First, he documented seed structure for many species, generally magnified 10–30 times, revealing testal features. He also discovered that at anthesis some species of Pachycereeae had idioblastic pigment cells in the funicular epidermis, which subsequently develop into spherical pigment cells in the fruit pulp. He termed these structures "pearl cells" (Perlzellen) because they appeared as colored beads on a colorless string (funiculus). Moreover, Buxbaum was keenly interested in the presence of triterpenes in some of these species, which had been biochemically investigated by Djerassi (1957; Gibson & Horak, 1978).

Buxbaum's first phylogenetic diagram of Pachycereeae (Fig. 1), which arranged the genera into five subtribes, differed in no substantial way from even the final version (Gibson & Horak, 1978), except that he eventually combined subtribes Stenocereinae and Cephalocereinae to form a larger Stenocereinae and also added *Machaerocereus* Britt. & Rose (Buxbaum, 1968) and *Rathbunia* Britt. & Rose (Buxbaum, 1975) to this subtribe as derivatives of *Stenocereus* (A. Berger)

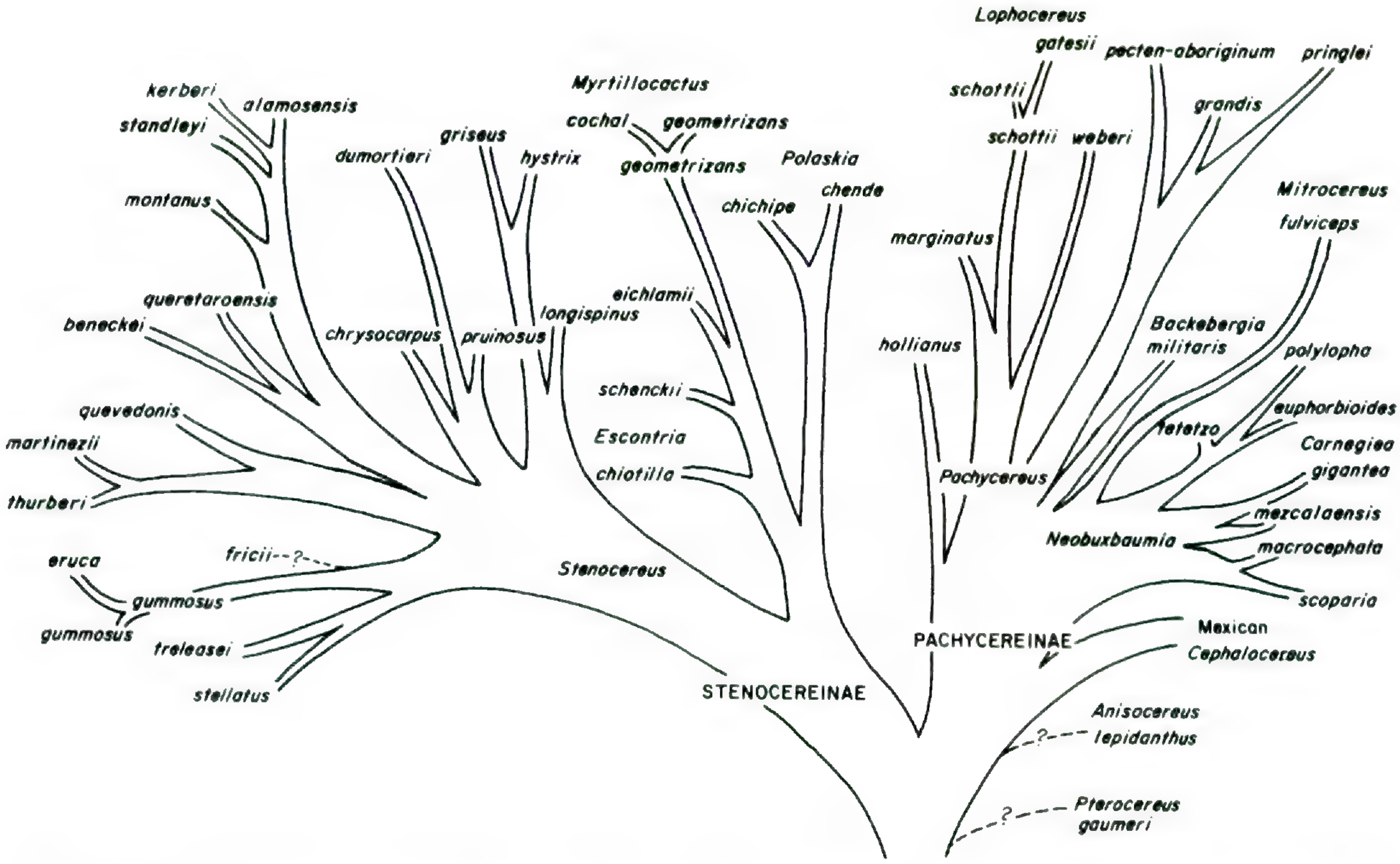


FIGURE 2. The original phylogenetic hypothesis of Pachycereeae by Gibson and Horak (1978), which recognized two major subtribes, Stenocereinae and Pachycereinae.

Riccob. Interestingly, Buxbaum used the presence of funicular pigment cells and of stem triterpenes as the chief criteria for including these two genera in Pachycereeae.

TESTING BUXBAUM'S MODEL

For many years population biologists have studied the evolutionary genetics and ecology of *Drosophila* living in rotting tissues of cacti, especially in the columnar cacti of the Sonoran Desert (Barker & Starmer, 1982). Some species of cactophilic *Drosophila* are host-specific, whereas others are found on several or many species of cacti. In 1974, the *Drosophila* scientists requested assistance from the senior author for information on the phylogenetic relationships of *Drosophila* host plants in Pachycereeae; consequently, the phylogenetic model of Buxbaum was examined.

None of the patterns in *Drosophila* speciation, host-plant preference, or host-plant chemistry could be logically explained by the phylogenetic model; consequently, a study was initiated to test the overall validity of Buxbaum's phylogenetic model for Pachycereeae. To do this, species lists were prepared from the literature for selected derived characteristics, such as glycosidic triterpenes (23 species), pearl cells (13 species), and alkaloids (6 species), and these were tested against the existing phylogeny for congruence. Three observations were made. (1) Buxbaum's model failed tests of parsimony for these sets of data. For example, in his model, species with abundant triterpenes were portrayed as derivatives of species with abundant alkaloids, and vice versa. (2) Species known to have abundant glycosidic triterpenes seemed to lack alkaloids, and those with abundant alkaloids generally lacked triterpenes. (3) All species known to have pearl cells also had abundant glycosidic triterpenes. Because there was no apparent biological link between the specialized pigment cells in the locule and colorless stem triterpenes, the coincidence of two apomorphic features in a group of species suggested that these species belong to a monophyletic taxon and that realignments would be required.

To aid in the production of new phylogenetic hypotheses, stem transections were studied from the majority of species in Pachycereeae as well as in some columnar species from other tribes. Gibson and Horak (1978) discovered silica bodies in the skin (epidermis plus hypodermis) of some Pachycereeae. Silica bodies are uncommon in plants and were previously unreported from Cactaceae, and in Pachycereeae they occurred only in species with abundant glycosidic triter-

penes (oleanane class) and pearl cells. Conversely, a different set of species in Pachycereeae that lacked pearl cells had prismatic crystals of calcium oxalate in the skin. Using these synapomorphies, combined with general data on plant morphology, anatomy, and chemistry, a new phylogenetic model was proposed (Fig. 2). Species having or thought to have abundant oleanane triterpenes and pearl cells were classified as subtribe Stenocereinae, whereas any taxon with calcium oxalate crystals or abundant stem alkaloids was classified in subtribe Pachycereinae.

In Stenocereinae sensu Gibson and Horak, all species possessing silica bodies were reclassified in the emended genus *Stenocereus,* including *Machaerocereus* and *Rathbunia* as well as the Backeberg segregates *Hertrichocereus, Isolatocereus, Marshallocereus, Neolemaireocereus,* and *Ritterocereus.* When *Lemaireocereus hollianus* was moved out of subtribe Stenocereinae, because it lacked the synapomorphic features, Gibson and Horak (1978) followed Buxbaum (1961) in recognizing this as a species of *Pachycereus.* Also included in subtribe Stenocereinae was *Myrtillocactus, Escontria* s.s. (excl. *Anisocereus lepidanthus*), and *Polaskia,* which was combined with the monotype *Heliabravoa.*

In Pachycereinae, all of the genera recognized by Buxbaum were retained (*Lophocereus, Pachycereus, Backebergia, Cephalocereus, Carnegiea, Mitrocereus,* and *Neobuxbaumia*), but the genera were clustered to explain the occurrence of synapomorphic structural features. Two species of *Pachycereus, P. marginatus* (DC.) Britt. & Rose (= *Marginatocereus* Backeb.) and *P. weberi* (Coult.) Backeb., had been classified by many authors as either species of *Lemaireocereus* or *Stenocereus*; but because they have abundant alkaloids and lack pearl cells, they were removed from Stenocereinae. *Pterocereus* and *Anisocereus* were placed at the base of the phylogenetic tree (Fig. 2) without defining precisely how these are related to the two subtribes.

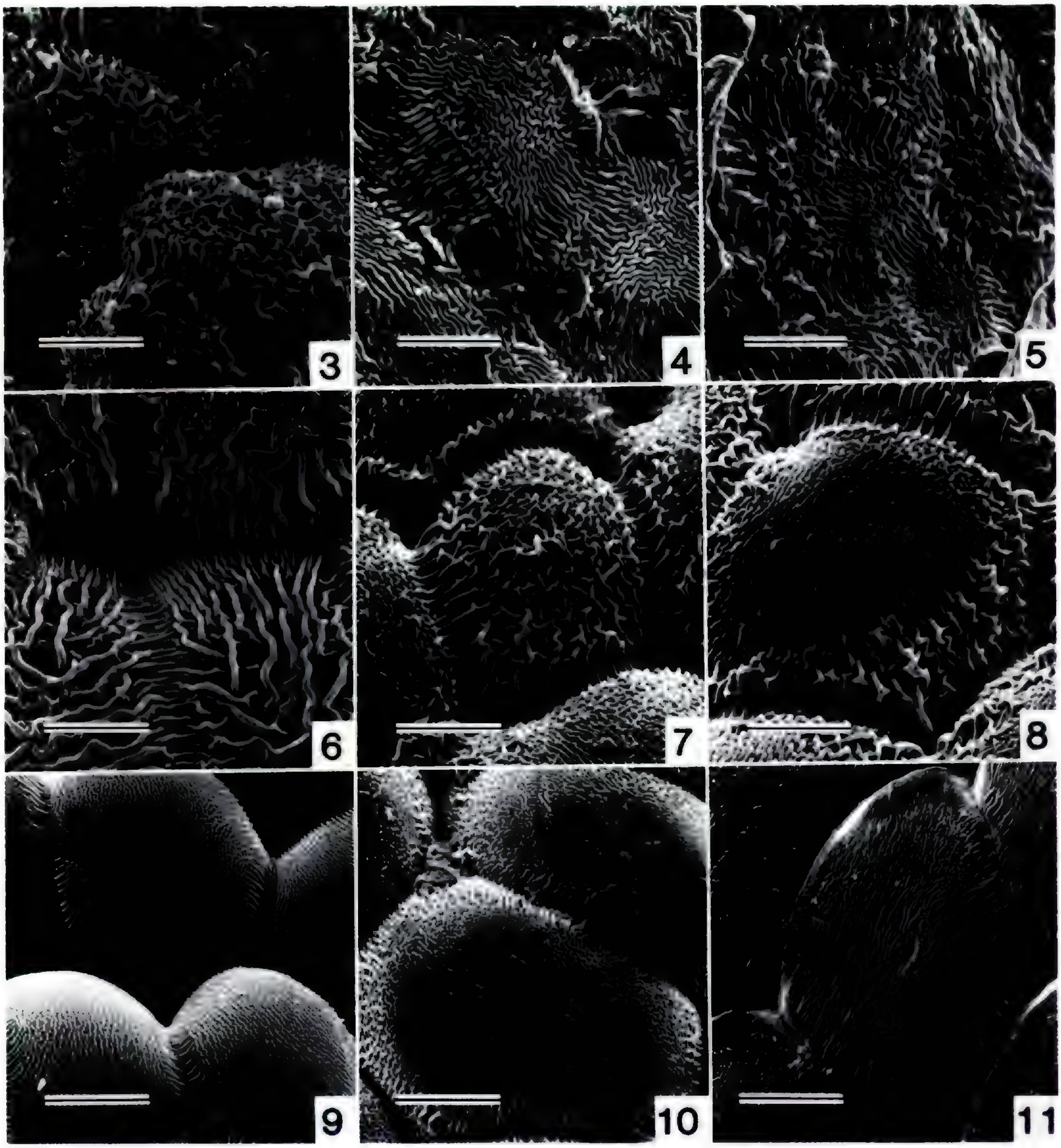
Gibson and Horak (1978) speculated on the proposed phylogenetic relationships of the species. Briefly, they suggested that speciation of these cacti fit an allopatric model, i.e., geographic speciation, in which the northern cacti, located in the Sonoran Desert, are the most highly derived and probably relatively recent species of seven different clades. Moreover, these cacti have many different floral designs that are adapted to use different types of pollinators, so that very closely related species often differ markedly in flower shape, length, color, position, and time of anthesis. The plethora of generic names in this tribe has resulted in part because previous authors emphasized the importance of external floral features for identifying taxa.

RECENT INVESTIGATIONS OF PACHYCEREEAE

Although Gibson and Horak (1978) were able to provide a fairly clear justification for reorganizing the species into monophyletic genera, the evidence for circumscribing subtribes, genera, and intrageneric groups was, to be sure, weak and incomplete. Any contemporary phylogeneticist viewing Figure 2, which was drawn in 1976, can see that this is not a precise statement of phylogenetic relationships of the species, especially in *Stenocereus.* Beginning in 1980, new vegetative and reproductive materials of Pachycereeae were collected in the field for structural and chemical analyses, with the goal that a cladistic model of the genera and species eventually could be produced. As new data were collected, some of the conclusions of Gibson and Horak were strongly reinforced, whereas others were clearly wrong or misguided and had to be discarded or modified.

Seed ultrastructure. The seeds of Pachycereeae were collected and examined with a scanning electron microscope to document testal sculpturing. Because data on seeds were very uneven and incomplete in Gibson and Horak (1978), a thorough study of seed ultrastructure was the first broad test of their phylogenetic model. *Lemaireocereus* sensu Britton and Rose (1920) exhibited a wide diversity of seed types, ranging from 4 mm to less than 0.5 mm long, brown to black, rough to smooth, and dull to glossy. As reconstituted, subtribe Stenocereinae Buxb. emend. Gibson & Horak basically included those species with relatively small, dull, rough seeds, called verrucose in recent accounts. However, the subtribe seemed to include several noteworthy exceptions.

Seeds of 22 species and one variety of the 30 species in subtribe Stenocereinae were analyzed, including any species whose seed morphology was not noticeably verrucose. Figures 3–11 show that all four genera have seeds characterized by convex cells with convex outer walls that have prominent cuticular striae, and the striae tend to traverse the cell margins (Figs. 3–9). This testal design was previously found in Pachycereeae by Leuenberger (1974) and Barthlott and Voit (1979)



FIGURES 3–11. Scanning electron photomicrographs of testa of Stenocereinae, showing characteristic cuticular striae.—3. *Escontria chiotilla* (Weber) Rose, *Gibson 3731* (RSA). Bar = 0.1 mm.—4. *Polaskia chende* (Gossel.) Gibson & Horak, *Gibson 3180* (ARIZ). Bar = 0.2 mm.—5. *Myrtillocactus geometrizans* (Mart.) Cons., *Gibson 3754* (RSA). Bar = 0.2 mm.—6. *Polaskia chichipe* (Gossel.) Backeb., *Gibson 3734* (RSA). Bar = 0.2 mm.—7. *Stenocereus pruinosus* (Otto) Buxb., *Gibson 3729* (RSA). Bar = 0.2 mm.—8. *Stenocereus pruinosus*; same seed as but different region than Figure 7, showing that cell size and prominence of striae varies considerably. Bar = 0.2 mm.—9. *Stenocereus quevedonis* (G. Ortega) Buxb., *Gibson 3713* (RSA). Bar = 0.2 mm.—10. *Stenocereus chrysocarpus* Sánchez Mejorada, *Gibson 3716* (RSA). Bar = 0.2 mm.—11. *Stenocereus thurberi* (Engelm.) Buxb., *Gibson 3751* (liquid-preserved voucher). Bar = 0.2 mm.

and is fairly widespread in Cactoideae (Barthlott & Voit, 1979; Barthlott, 1981; Behnke & Barthlott, 1983). On the very small seeds of *Myrtillocactus* and *Polaskia chende* (Gossel.) Gibson & Horak (Figs. 4–5), striae are fairly low but are still quite evident; and in some species of *Stenocereus*, the striae in the center of each cell may be reduced so that the surface appears fairly smooth. In *Stenocereus thurberi*, which superficially appears to have smooth, black seeds, the

testal cells are somewhat flattened but still retain striae (Fig. 11). In *S. alamosensis* (Coult.) Gibson & Horak (Fig. 12) the seed coat is very smooth except between the cells, where faint striae can be observed to cross the cell margins. Once again, the closely related species *S. kerberi* (Schum.) Gibson & Horak and *S. standleyi* (G. Ortega) Buxb. have typical seed features of *Stenocereus*. Finally, in *S. beneckei* (Ehrenb.) A. Berger & Buxb. (Fig. 13), which has the largest seeds in the subtribe (3 mm) and the thickest testa, the testa lacks well developed rugae and striae but is still quite rough. *Stenocereus beneckei* has the vast majority of features found in the genus, including silica bodies, abundant triterpenes, and red areolar trichomes but no pearl cells. Each of these deviations from the standard testal design of Stenocereinae can be explained as a secondary modification.

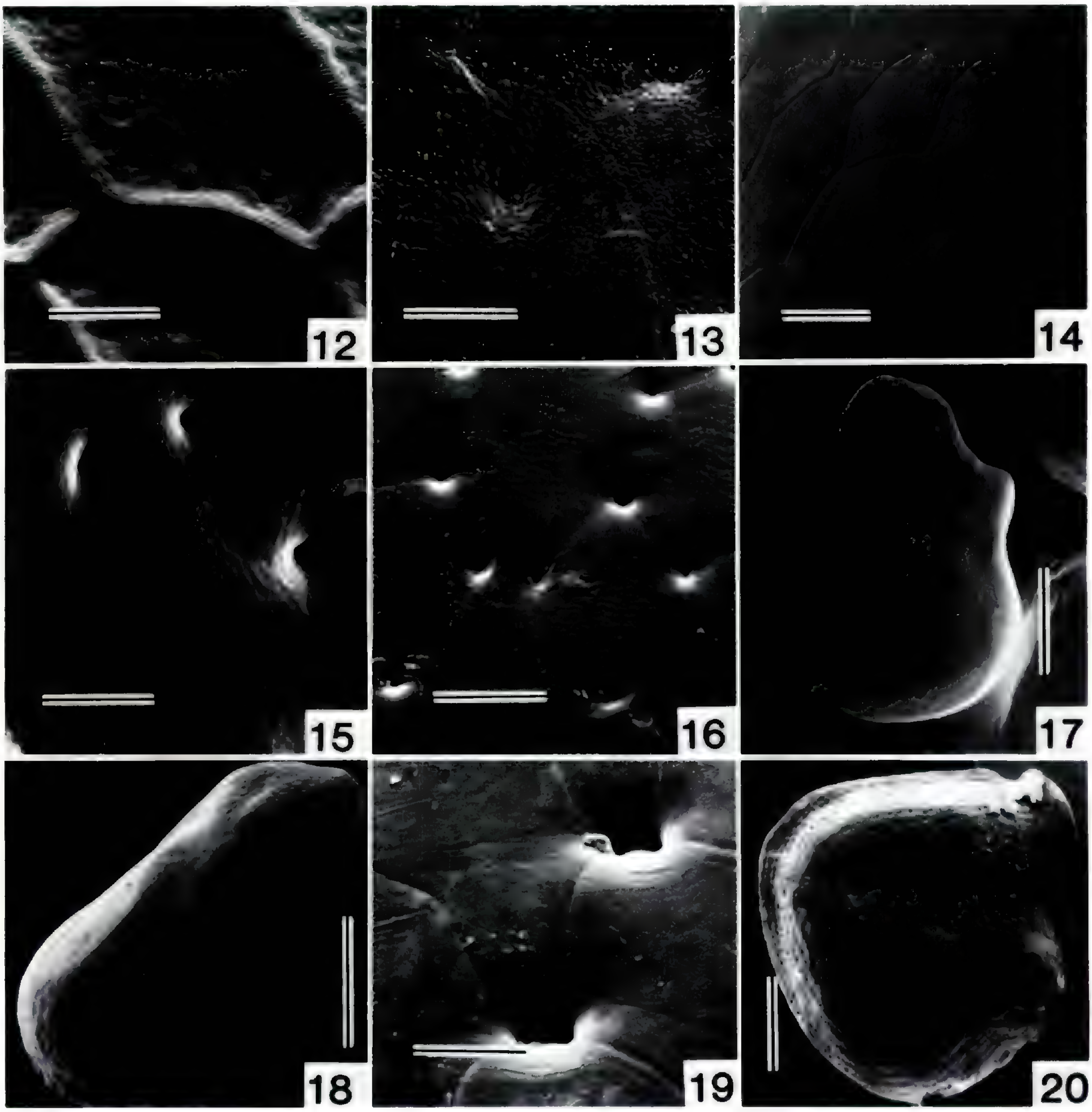
In species assigned to Pachycereinae, none of the seeds are dull or rough. On these seeds (Figs. 14–20), the cuticle is smooth, and the cells bulge outward only slightly or are flat. In some species of *Pachycereus,* the outlines of the cells are difficult to distinguish (Figs. 15–20); but in *P. marginatus* (Fig. 15) and *P. weberi* (Fig. 16), deep pits form at the cell corners. Only in certain species of *Cephalocereus* have striae been observed traversing the cell margins, in a manner similar to *S. alamosensis*. There does not seem to be a single seed type or testal design characteristic of all Pachycereeae as presently defined, and especially the seed of *Pachycereus hollianus* (Fig. 20) is atypical of the subtribe.

Morphological distinctiveness of seeds, fruits, and stem of *P. hollianus* were reanalyzed when Unger et al. (1980) surveyed tetrahydroisoquinoline alkaloids in eight species of Pachycereinae but reported none in *P. hollianus,* whereas the other species of *Pachycereus* had many important alkaloids. Consequently, Gibson (1982) recommended that the old name, *Lemaireocereus hollianus,* be used to recognize a monotypic genus of Pachycereinae and presumably a sister taxon of *Pachycereus*.

Stem triterpenes. In Gibson and Horak (1978), stem triterpene data obtained earlier by Djerassi played a key role in the reorganization of the species into subtribes, and the distribution of triterpene skeletons was used to evaluate the intrageneric relationships of species in Stenocereinae. However, plant chemotaxonomists should compare taxa by using the glycosidic forms of secondary compounds, the actual plant compounds, because the glycosides have maximum information content (Giannasi, 1978; Crawford & Mabry, 1978; Stuessy & Crawford, 1983; Spencer & Siegler, 1985).

A fairly simplistic survey was made of triterpene chemistry of 20 available species of Stenocereinae and four other species of columnar cacti, first to determine whether they have abundant triterpenes and then to estimate the overall similarity of the glycosidic triterpenes of the species. Extractions were made in the field by grinding pieces of cortex with skin and spines of young, vigorous shoots in a blender with 95% ethanol. Each extract was filtered and concentrated in a flask evaporator to a thick syrup, and the syrup was partitioned between water, ethyl acetate, and ether to remove waxes. Triterpenes and carotenoids that appeared in the ethyl acetate fraction were chromatographed on silica gel thin-layer chromatographic plates in a variety of solvents, including 10 : 1, chloroform : methanol, 1 : 1, hexane : ethyl acetate, and 100 : 100 : 1, n-heptane : benzene : methanol. Compounds were detected with Lieberman-Burchard reagent and vanillin reagent and examined with UV light. From these extractions, a total of over 50 distinct compounds tested positive as triterpenes. These new phytochemical studies revealed abundant triterpenes in four species of Stenocereinae that had not been investigated by Djerassi, *S. kerberi, S. fricii* Sánchez Mejorada, *S. chrysocarpus* Sánchez Mejorada, and *S. standleyi,* and also from the plant called *Lemaireocereus thurberi* (Engelm.) Britt. & Rose var. *littoralis* (K. Brandeg.) Linds. We also detected large numbers of triterpenes in *Bergerocactus emoryi* and several triterpenes in *Lemaireocereus humilis* Britt. & Rose, but *Pterocereus gaumeri* (Britt. & Rose) MacDoug. & Miranda lacked triterpenes and *Mitrocereus fulviceps* (Weber) Backeb. ex Buxb. produced one equivocal band. Hence, the presence of abundant glycosidic triterpenes was verified as a good marker for Stenocereinae, because in the 25 species (out of 30) that have been tested, all possess abundant triterpenes. The presence of many, apparently different triterpenes in *Bergerocactus* needs intensive study.

Because samples provided were small, isolation and chemical identification of the glycosidic triterpenes were not attempted. Instead, a small set of intraspecific and interspecific comparisons was conducted to estimate the relative similarity of taxa within the subtribe. Three or four species were run simultaneously on each thin-layer chro-



FIGURES 12–20. Scanning electron photomicrographs of testa of Pachycereeae.—12. *Stenocereus alamosensis* (Coult.) Gibs. & Horak, *Gibson 3709* (RSA); testa is fairly smooth, but faint striae traverse the cell margins. Bar = 0.2 mm.—13. *Stenocereus beneckei* (Ehrenb.) Berg. & Buxb., *Gibson 3726* (RSA). Bar = 0.2 mm.—14. *Pachycereus pringlei* (S. Wats.) Britt. & Rose, *Gibson 3629* (liquid-preserved voucher). Bar = 0.1 mm.—15. *Pachycereus marginatus* (DC.) Britt. & Rose var. *gemmatus* (Zucc.) Bravo, *Gibson 3722* (liquid-preserved voucher); deep pits form at cell junctions. Bar = 0.2 mm.—16. *Pachycereus weberi* (Coult.) Backeb., *Gibson 3721* (RSA). Bar = 0.1 mm.—17. *Lophocereus schottii* (Engelm.) Britt. & Rose, *Gibson 3195* (ARIZ); seed with slightly convex cell walls and smooth cuticle. Bar = 1 mm.—18. *Cephalocereus hoppenstedtii* (Weber) K. Schum., *Gibson 3741* (RSA); this seed has a fairly well-developed raphe. Bar = 1 mm.—19. *Lemaireocereus hollianus* (Weber) Britt. & Rose, *Gibson 3735* (RSA). Bar = 0.2 mm.—20. *Lemaireocereus hollianus*; same seed as Figure 19, showing that this has a different shape than other Pachycereeae. Bar = 1 mm.

matographic plate, and the sequence of bands on each plate was then compared using color reagents in a qualitative way. The conclusions drawn from these tests are, of course, very crude for estimating phylogenetic relationships, but informative (Fig. 21).

1. The 14 species of *Stenocereus* tested shared a common pattern of triterpene glycosides.

2. *Stenocereus stellatus* and *S. treleasei* (Britt. & Rose) Backeb. were essentially the same, and *S. stellatus* was also very similar to *S. gummosus*.

3. *Stenocereus standleyi* and the two rathbunias, *S. kerberi* and *S. alamosensis,* seemed to be identical in triterpenes. These three species were examined more closely with trial separation performed on a silica gel column using an ascending polar solvent system. Each specimen had 30 bands, which all appeared to be the same. This group of three species was most similar to the *S. stellatus* group. The two populations of *S. alamosensis* examined were identical.

4. The nine taxa tested that have glandular areolar trichomes, e.g., *S. thurberi* and *S. queretaroensis* (Weber) Britt. & Rose, were more similar to each other than they were to the previous two groups.

5. Within the taxon with glandular areolar trichomes, there were two groups, one with columnar cacti centered in Nueva Galicia (*S. fricii* to *S. chrysocarpus*) and another that reaches to the Sonoran Desert (*S. thurberi* and relatives).

6. Triterpene glycosides of *S. thurberi* appeared to be identical to those of "*Lemaireocereus thurberi* var. *littoralis,*" which has been treated either as a variety of organ pipe cactus or a distinct species but does not yet have a *Stenocereus* name.

7. Two species, *S. eruca* (Brandeg.) Gibson & Horak and *S. dumortieri* (Scheidweil.) Buxb., had a number of unusual triterpenes, and decisions on these could not be made for placing them with any of the species groups.

8. The two species of *Polaskia* had relatively few, simple, and similar triterpene glycosides.

9. Both *Escontria chiotilla* (Weber) Rose and the three species of *Myrtillocactus* differed markedly from and were more complex than *Polaskia.*

10. *Escontria, Polaskia,* and *Myrtillocactus* shared some compounds with *Stenocereus.*

The results yielded no real taxonomic applications, but they should be compared with earlier statements on the presumed relationships of these species. The close similarity of the three species in the rathbunia alliance based on 30 triterpene bands lends support to elimination of *Rathbunia,* which was previously argued on morphological grounds. Next, according to these data, *S. gummosus* is most closely related to *S. stellatus.* Gibson and Horak (1978) had presumed that the sister taxon of *S. gummosus* (Engelm.) Gibson & Horak was *S. fricii,* based solely on examination of literature accounts. Another northern cactus, *S. thurberi,* does appear to be related to *S. quevedonis* (G. Ortega) Buxb., as suggested in Gibson and Horak (1978), but *S. beneckei* should

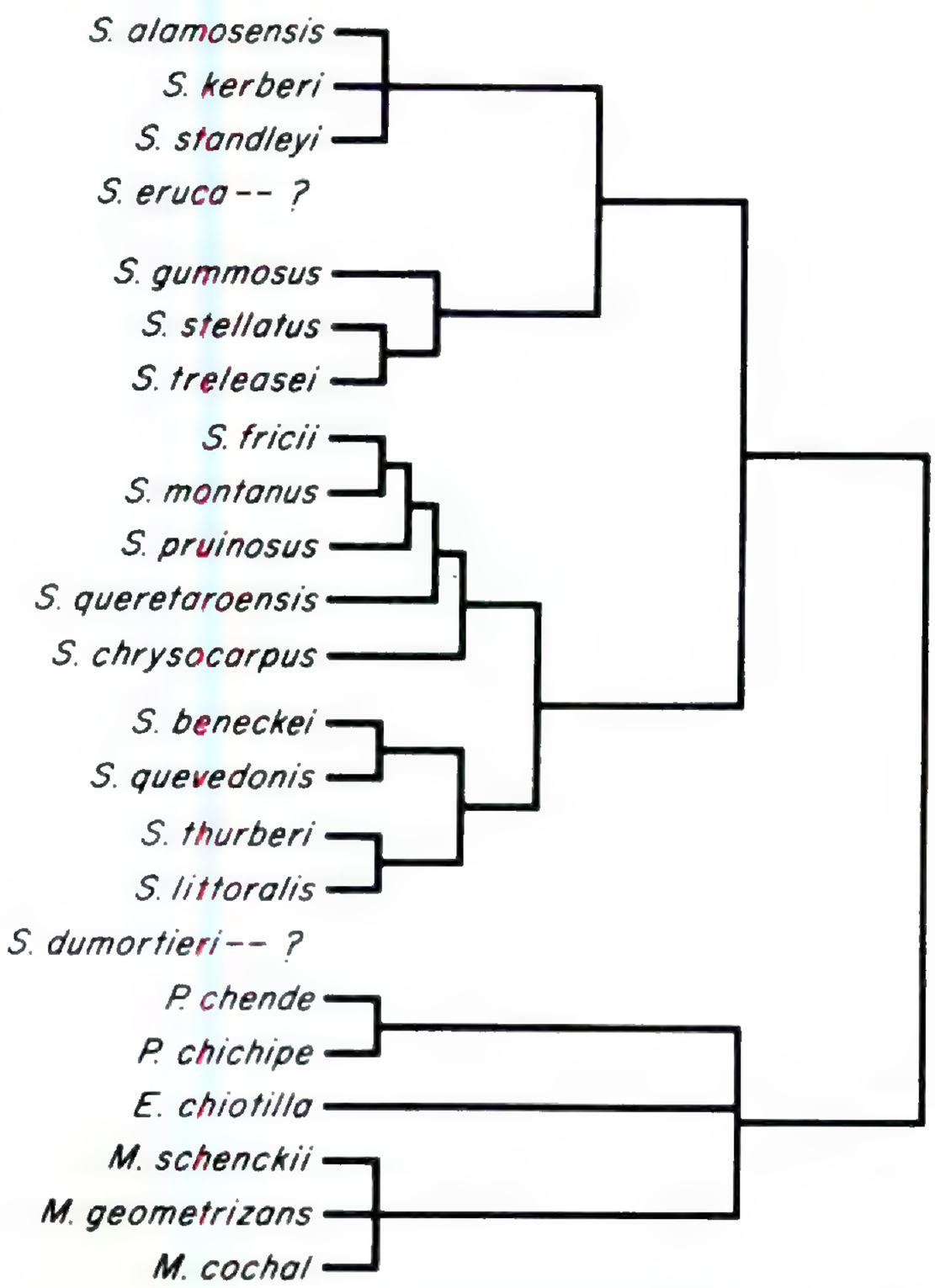


FIGURE 21. Crude dendrogram that shows the qualitative similarities of glycosidic triterpenes found in 21 taxa of Stenocereinae. *S.* = *Stenocereus, P.* = *Polaskia, E.* = *Escontria, M.* = *Myrtillocactus.*

be considered as a member of this group. *Stenocereus eruca* has always been treated as a derivative of *S. gummosus,* because both have similar flowers, fruits, and spines and occur in Baja California. This may be correct, but additional studies are needed to explain why the stem chemistry of these two species is so different.

Stem flavonoids. Research on flavonoids in cacti has been overshadowed by that on betalain pigments, which are unique in the Centrospermae (Mabry, 1976). Recently, several authors have reviewed data on flavonoids from cactus flowers and stems (Clark & Parfitt, 1980; Burret et al., 1981; Miller & Bohm, 1982), but flavonoids had not been studied in Pachycereeae.

To determine the relative value of flavonoids for phylogenetic models of Pachycereeae, a very simplistic survey was conducted using the same ethanol extractions obtained for triterpene analysis. A survey of flavonoids was conducted using two-dimensional paper chromatography; and R_f values and standard indicator sprays viewed under UV light were used to analyze the results. Surprisingly, over 200 distinct flavonoids were

TABLE 2. Columnar cacti tested for alkaloids from ethanol or $CHCL_3$ extracts. All species except "*Lemaireocereus humilis,*" sometimes called *Armatocereus humilis,* are currently classified in tribe Pachycereeae. Authorities for all taxa appear in Gibson and Horak (1978).

Taxon	Voucher or Source	Wt. of Dry Plant Material/g	Wt. of Alcoholic/ Chloroform Extract	Wt. of Fractions/mg		
				B	A	C
Ethanol Extracts						
1. *Backebergia militaris*	*Gibson 3717* (RSA)	19.7	4.7	85.0	246.0	290.0
2. *Cephalocereus chrysacanthus*	*Gibson 3743* (RSA)	19.7	2.3	125.0	32.5	99.5
3. *C. collinsii*	*Gibson 3742* (RSA)	22.0	2.89	89.0	42.0	95.0
4. *C. hoppenstedtii*	*Gibson 3741* (RSA)	44.6	3.1	184.0	8.0	158.5
5. *C. purpusii*	*Gibson 3710* (RSA)	15.0	3.8	99.0	200.0	199.5
6. *C. senilis*	*Gibson 3750* (RSA)	17.8	2.0	120.0	9.0	97.5
7. *C. totolapensis*	*Gibson 3740* (RSA)	26.3	2.4	129.0	7.0	77.5
8. *Escontria chiotilla*	*Gibson 3751* (RSA)	28.7	12.6	341.0	78.0	300.0
9. *Lemaireocereus hollianus*	*Gibson 3735* (RSA)	6.7	0.9	30.0	39.0	310.0
10. *Mitrocereus fulviceps*	*Gibson 3744* (RSA)	11.5	1.5	180.0	8.0	115.0
11. *Neobuxbaumia macrocephala*	*Gibson 3745* (RSA)	36.2	6.1	247.0	7.0	92.5
12. *N. mezcalaensis*	*Gibson 3725* (RSA)	56.5	3.4	246.0	12.5	140.5
13. *N. mezcalaensis*	*Gibson 3756* (RSA)	23.8	3.7	98.5	5.0	94.0
14. *N. tetetzo*	*Gibson 3737* (RSA)	29.5	2.4	201.5	7.0	32.5
15. *Pachycereus grandis*	*Gibson 3749* (RSA)	21.4	1.2	403.0	45.3	167.0
16. *P. marginatus marginatus*	*Gibson 3755* (RSA)	6.2	2.1	90.0	150.0	196.0
17. *P. pecten-aboriginum*	*Gibson 3748* (RSA)	15.9	1.3	128.5	44.0	93.0
18. *P. weberi*	*Gibson 3728* (RSA)	15.1	1.2	72.6	84.5	173.0
19. *P. weberi*	*Gibson 3721* (RSA)	15.9	1.2	173.0	29.0	180.5
20. *Stenocereus dumortieri*	*Gibson 3727* (RSA)	22.3	11.0	85.0	67.0	320.0
$CHCL_3$ Extracts						
21. *Lemaireocereus humilis*	*Gibson 3183* (ARIZ)	10.0	0.25	21.0	13.5	14.5
22. *Neobuxbaumia polylopha*	Huntington Botanical Garden	15.0	1.5	9.0	8.0	4.5
23. *Pachycereus grandis*	*Gibson 3749* (RSA)	15.0	0.20	19.5	11.0	11.0
24. *P. pecten-aboriginum*	40 km south of Ciudad Obregon, Sonora, Mexico	20.0	0.70	55.5	105.5	87.5
25. *Polaskia chende*	*Gibson 3180* (ARIZ)	5.0	1.75	submitted for mass spec./mass spec. analysis		
26. *Pterocereus gaumeri*	Huntington Botanical Garden	6.96	0.20	24.0	24.0	31.0
27. *Stenocereus beneckei*	Huntington Botanical Garden	5.0	0.13	submitted for mass spec./mass spec. analysis		
28. *S. stellatus*	Huntington Botanical Garden	5.0	0.18	submitted for mass spec./mass spec. analysis		

detected from the 24 species, and on a chromatograph of *Stenocereus thurberi,* there were at least 70 distinct spots. Most specimens had more than 40 distinct phenolic compounds. This apparent diversity is remarkable because the studies of other Cactaceae have included few reports of flavonoids in stem tissues. No attempt was made to identify these phenolic compounds be-

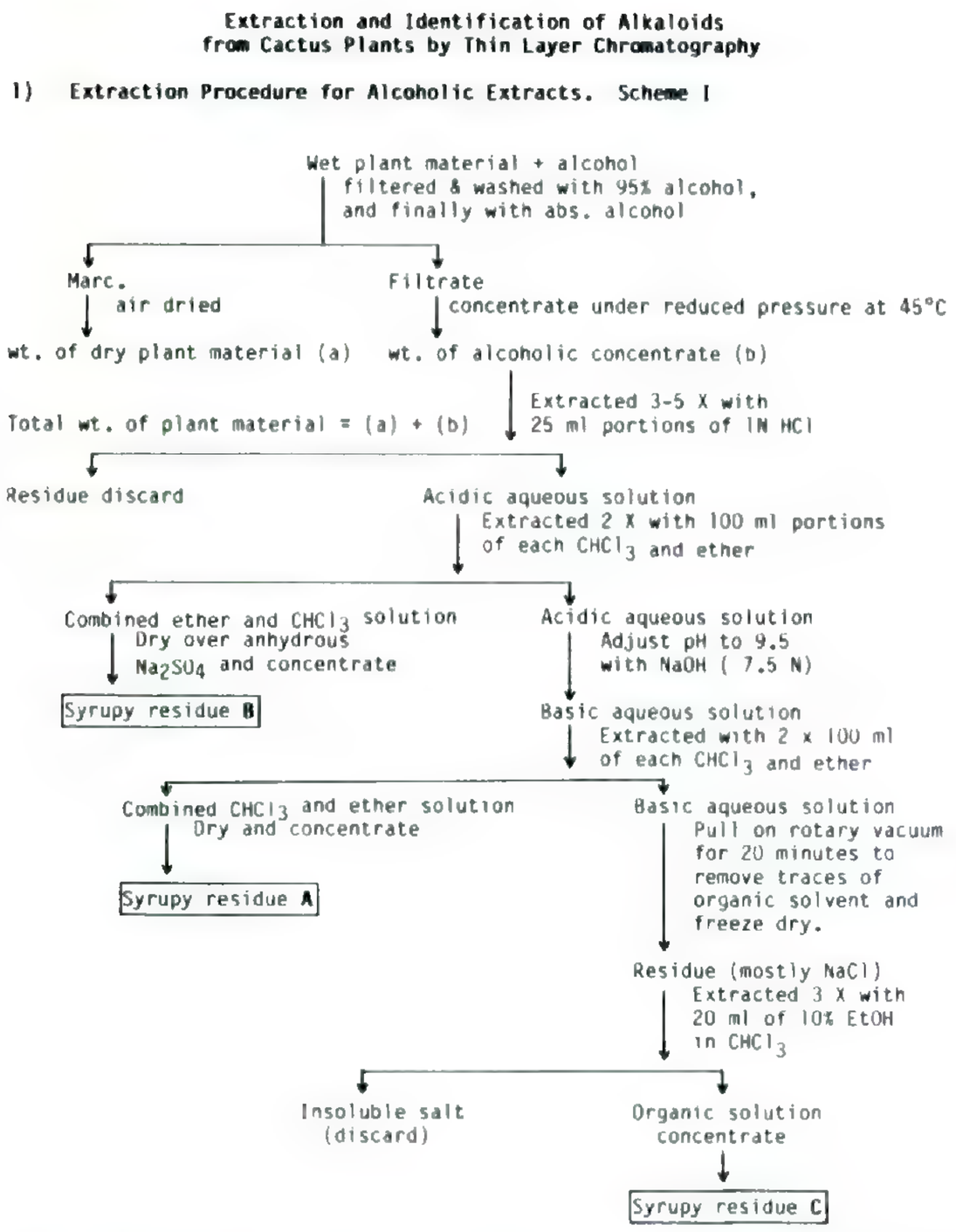


FIGURE 22. Flow chart of the extraction and identification of alkaloids from cactus stems by thin-layer chromatography using ethanolic extracts (Scheme I).

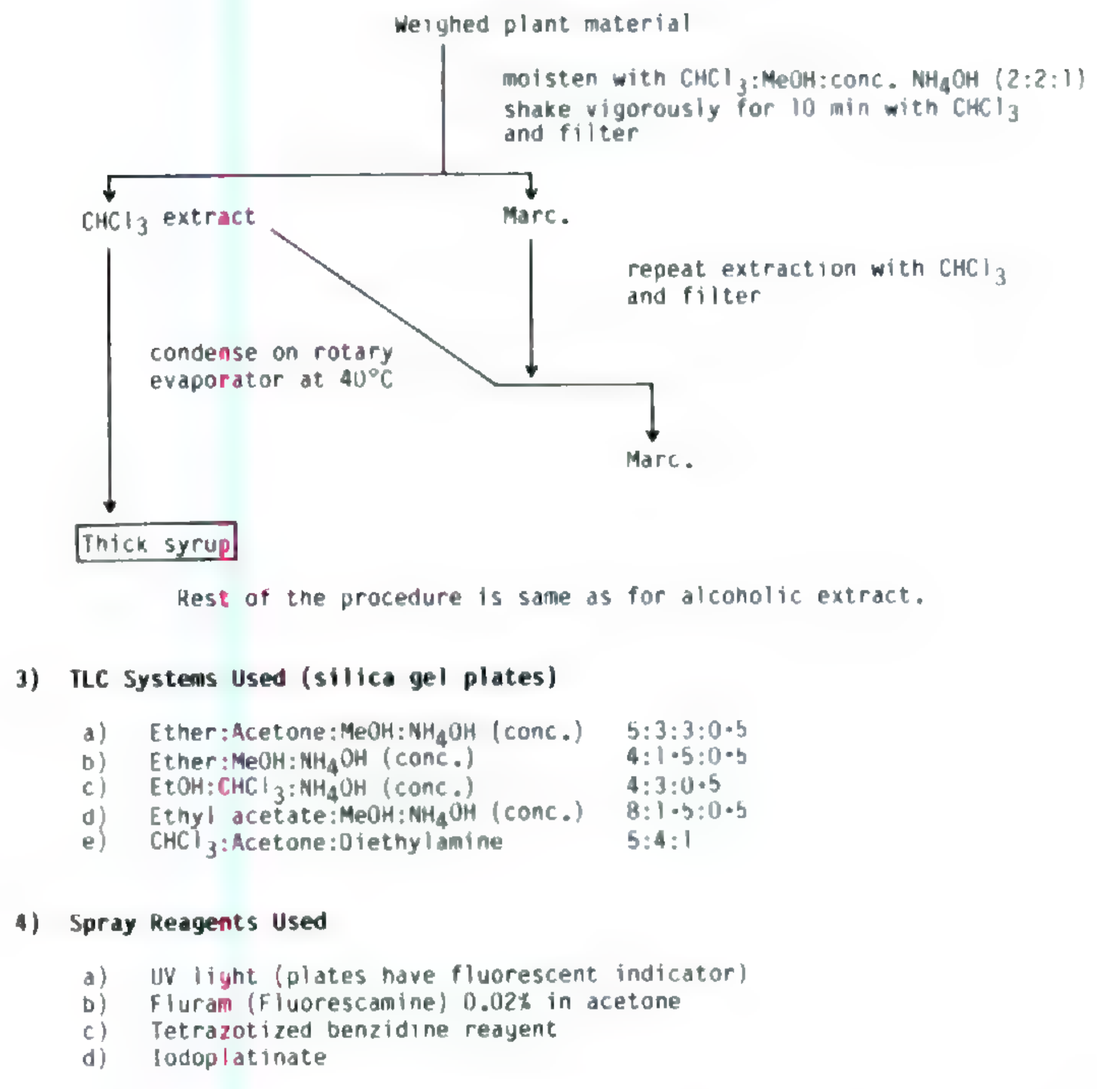


FIGURE 23. Flow chart of the extraction and identification of alkaloids from cactus stems by thin layer chromatography using powdered materials obtained from fresh plants (Scheme II).

cause there were so many and because the samples and sample sizes were very small. Nevertheless, comparisons among *S. standleyi, S. kerberi,* and *S. alamosensis* revealed 41 visually identical spots, many of which were not present in other species. This observation reinforces the previous statement based on the visual similarities of 30 triterpenes, and these and morphological evidence suggest that these three species are not only closely related but also fairly recent segregates.

Stem alkaloids. Prior to 1977 alkaloids had been detected in seven species of Pachycereeae (Djerassi et al., 1953, 1954, 1956, 1958, 1972; Agurell, 1969; Bruhn et al., 1970; Bruhn, 1971; Bruhn & Lindgren, 1976; Bruhn & Lundström, 1976). Most research had concentrated on these unique tetrahydroisoquinoline alkaloids.

The phylogenetic hypothesis of Gibson and Horak (1978) placed all known alkaloid-bearing species of this tribe in Pachycereinae, and this model inferred that other alkaloid-bearing species should occur in that subtribe. The model was immediately tested for this prediction, and investigators found abundant and even new alkaloids in the chemically unknown *Backebergia militaris* (Audot) Bravo ex Sánchez Mejorada (Mata & McLaughlin, 1980a; Pummangura & McLaughlin, 1981) as well as in species that had not been examined very closely (Mata & McLaughlin, 1979, 1980b, 1980c). Alkaloids known from Pachycereinae before 1981 are listed in Mata and McLaughlin (1982).

Extractions were made in the field for 16 species of Pachycereinae and two species of Stenocereinae (Table 2) by grinding pieces of cortex with skin and spine of young, vigorous shoots in a blender with 95% ethanol. These were then analyzed using the isolation procedure outlined in Scheme I of Figure 22, and all recovered fractions (A–C) were tested for alkaloids. In addition, chloroform extractions were made from powdered (freeze-dried fresh) stems of nine species (Table 2) using Scheme II in Figure 23. Methods used for identifying the alkaloids have been published previously (Ranieri & McLaughlin, 1976).

Table 3 lists the alkaloids identified by thin-layer chromatography from these samples, and Figures 24 and 25 show the chemical structure of each alkaloid. This survey demonstrated that alkaloids are present in some species of *Cephalocereus, Neobuxbaumia mezcalaensis* (Bravo) Buxb., and *Pachycereus grandis* Rose, which had not previously been tested. However, the survey made two other important findings. First, it showed that not all Pachycereinae have alkaloids, because alkaloids could not be detected in

TABLE 3. Alkaloids identified from columnar cacti (Table 2) by Bajaj and McLaughlin using thin-layer chromatography. Each alkaloid cochromatographed and gave identical visualization reactions with reference alkaloids in all (at least three) solvent systems tested.

Species	Alkaloids Identified by TLC	Fraction/ A/B/C
1. *Backebergia militaris*	1) Backebergine (traces)	A
	2) Dehydroheliamine	A
	3) 3,4-dimethoxy PEA	A/C
	4) Lemaireocereine (traces)	A
	5) N,N-dimethyl-3,4-dimethoxy PEA	A
	6) Heliamine	A
	7) N-methyl-3,4-dimethoxy PEA	A
2. *Cephalocereus chrysacanthus*	1) N,N-dimethyl-3,4-dimethoxy PEA	A
	2) N-methyl-3,4-dimethoxy PEA	A
3. *Cephalocereus collinsii*	1) N,N-dimethyl-3,4-dimethoxy PEA	A
	2) N-methyl-3,4-dimethoxy PEA	A
4. *Cephalocereus hoppenstedtii*	1) N-methyl-3,4-dimethoxy PEA (traces)	A
5. *Cephalocereus purpusii*	1) Tyramine	A
	2) N-methyl-3,4-dimethoxy PEA	A
	3) Dehydroheliamine	A
	4) three unidentified alkaloids	A/C
6. *Cephalocereus senilis*	No alkaloid	
7. *Cephalocereus totolapensis*	No alkaloid	
8. *Escontria chiotilla*	One unidentified polar secondary alkaloid	A/C
9. *Lemaireocereus hollianus*	1) N,N-dimethyl-3,4-dimethoxy PEA (traces)	A
	2) N-methyl-3,4-dimethoxy PEA (traces)	A
	3) 3,4-dimethoxy PEA	A
	4) 3-methoxytyramine	C
	5) N-methoxy-3-methoxytyramine	C
10. *Mitrocereus fulviceps*	No alkaloid	
11. *Neobuxbaumia macrocephala*	No alkaloid	
12. *N. mezcalaensis*	One unidentified alkaloid (traces)	
13. *N. mezcalaensis*	1) Heliamine (traces)	C
14. *N. tetetzo*	No alkaloid	
15. *Pachycereus grandis*	No alkaloid	
16. *Pachycereus marginatus marginatus*	1) Pilocereine	A
	2–3 unidentified alkaloids	A
17. *Pachycereus pecten-aboriginum*	1) Heliamine	A
	2) Salsoline	A
	3) 3,4-dimethoxy PEA (traces)	A
	4) 3-methoxytyramine	A
18. *P. weberi*	1) Dehydroheliamine (conc.)	A/C
	2) Tehuanine (conc.)	A
	3) Pellotine (traces)	A
	4) Lemaireocereine (traces)	A
	5) Weberidine (traces)	A
	6) Nortehuanine	A
	7) Anhalonidine	A/C
	8) Heliamine	A/C
19. *P. weberi*	1) Dehydroheliamine	A
	2) Tehuanine	A
	3) 3-methoxytyramine	A/C
	4) Tyramine (traces)	C
20. *Stenocereus dumortieri*	Traces of two unidentified alkaloids	A
21. *Lemaireocereus humilis*	No alkaloid	

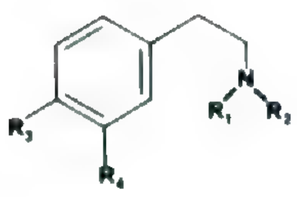
TABLE 3. Continued.

Species	Alkaloids Identified by TLC	Fraction/ A/B/C
22. *Neobuxbaumia polylopha*	No alkaloid	
23. *Pachycereus grandis*	1) Tehuanine	A
	2) O-methylpellotine	A
	3) N-methylheliamine (traces)	A
	4) Carnegine	A
24. *P. pecten-aboriginum*	1) Tehuanine (traces)	A
	2) O-methylpellotine	B/A
	3) Carnegine (conc.)	B/A/C
	Two unidentified alkaloids	B/A
25. *Polaskia chende*	One primary alkaloid	A/C
26. *Pterocereus gaumeri*	1) Deglucopterocereine	A/C
	Two unidentified tertiary alkaloids (high conc.)	A/C
27. *Stenocereus beneckei*	One primary alkaloid	A/C
28. *S. stellatus*	Three primary alkaloids	A/C

Mitrocereus fulviceps, four species of *Neobuxbaumia,* and several species of *Cephalocereus,* including the type, *C. senilis* (Haw.) Pfeiff. Second, alkaloids were discovered in Stenocereinae. To date, primary alkaloids have been detected in *Polaskia chende, Stenocereus beneckei, S. dumortieri, S. stellatus,* and *S. treleasei*; whereas *Escontria chiotilla* from Puebla contained an unidentified secondary alkaloid. Moreover, *S. eruca* showed a positive test with commonly used alkaloid indicators.

The tetrahydroisoquinoline alkaloids have been found in all species of *Pachycereus, Lophocereus, Backebergia,* and *Carnegiea,* in *Pterocereus gaumeri,* two species of *Cephalocereus,* and *Neobuxbaumia mezcalaensis,* whereas the simpler alkaloids of tyramine and phenethylamine occur in most of these same species as well as in *Lemaireocereus hollianus* and numerous species of *Cephalocereus* (Mata & McLaughlin, 1982). The high diversity of tetrahydroisoquinoline alkaloids (about 25 different compounds) in this group is in sharp contrast to their poor representation in other cactus taxa; and the occurrence of these secondary metabolites in the genera *Pachycereus, Lophocereus,* and *Backebergia* is a fairly good indicator that these genera are closely related, especially because these taxa possess other synapomorphic morphological and anatomical features. In addition, fresh stems of all five species of *Pachycereus* and *Backebergia* turn red and then blacken rapidly when they are cut, which in *P. weberi* was shown to be caused by the hydrolysis of the glucoside lemairin (Mata & McLaughlin, 1980d). Of the species rich in tetrahydroisoquinolines, *Lophocereus* and *P. marginatus* are chemically very similar and distinct from the rest of the species, which frequently share the same compounds. In contrast, *Carnegiea,* which superficially appears to share many alkaloids with *Pachycereus,* can be distinguished from the other species because it has different isomers of tetrahydroisoquinolines, suggesting that a different biosynthetic pathway may be involved (Unger et al., 1980); also, cut stems of *Carnegiea* blacken very slowly. *Pterocereus* has two unique alkaloids; however, this observation cannot be used as evidence for or against inclusion of this genus in Pachycereinae.

The abundance of primary alkaloids in Pachycereinae is an unreliable feature for analyzing relationships within the Pachycereinae because these are not only absent in some of the species but also are widespread compounds in all three subfamilies of Cactaceae, e.g., mescaline, the peyote hallucinogen (Doetsch et al., 1980). Primary alkaloids have now been discovered in six species of *Cephalocereus* s.l., including *C. hoppenstedtii* but not in the very closely related type species, *C. senilis,* and not in *C. totolapensis,* which has been classified as the genus *Neodawsonia* Backeb. Because *Mitrocereus fulviceps* and the species of *Neobuxbaumia* are not rich in stem alkaloids and share the pattern of calcium oxalate crystals in the skin, all of these Pachycereinae species that lack abundant tetrahydroisoquinoline alkaloids appear to be a clade, separate from the clade of *Lophocereus, Backebergia,* and *Pachycereus.* Placement of the alkaloid-rich *Carnegiea* and of *Lemaireocereus hollianus* is still



R_1,R_2,R_4=H; R_3=OH: tyramine

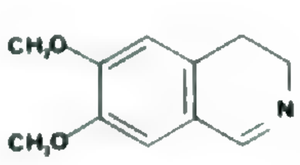
R_1,R_2=H; R_3,R_4=CH_3O: 3,4-dimethoxy PEA

R_1=CH_3; R_2=H; R_3,R_4=CH_3O: N-methyl-3,4-dimethoxy PEA

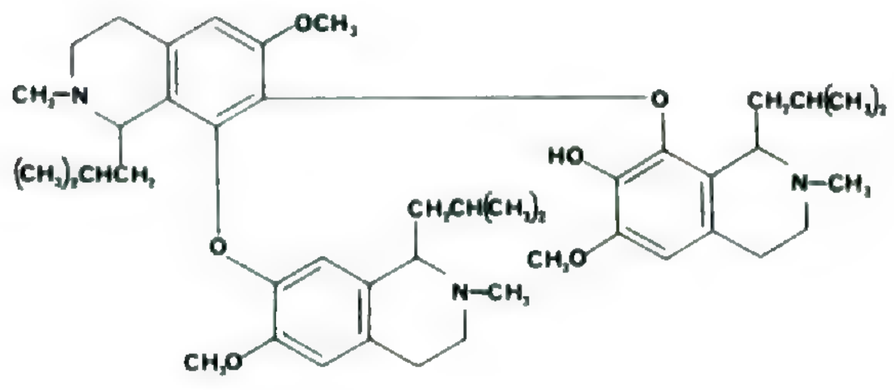
R_1,R_2=CH_3; R_3,R_4=CH_3O: N,N-dimethyl-3,4-dimethoxy PEA

R_1,R_2=H; R_3=OH; R_4=OCH_3: 3-methoxytyramine

R_1=H; R_2=CH_3; R_3=OH, R_4=OCH_3: N-methyl-3-methoxytyramine

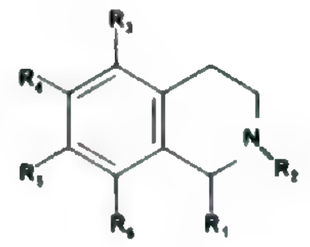


dehydroheliamine



pilocereine

FIGURE 24. Alkaloids isolated from columnar cactus stems (Tables 2 and 3).



R_1=CH_3; R_2=H; R_3=H; R_4=OH; R_5=CH_3O; R_6=H: salsoline

R_1,R_1=H; R_3=H; R_4,R_5=CH_3O; R_6=H: heliamine

R_1,R_2,R_3,R_4=H; R_5,R_6=CH_3O: lemaireocereine

R_1=H; R_2=CH_3; R_3,R_4,R_5=CH_3O; R_6=H: tehuanine

R_1,R_2=CH_3; R_3=H; R_4,R_5=CH_3O; R_6=OH: pellotine

R_1,R_2,R_3,R_4=H; R_5=CH_3O; R_6=H: weberidine

R_1,R_2=H; R_3,R_4,R_5=CH_3O; R_6=H: nortehuanine

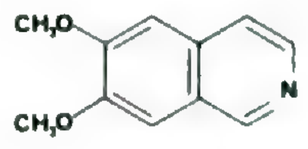
R_1=CH_3; R_2,R_3=H; R_4,R_5=CH_3O; R_6=OH: anhalonidine

R_1,R_2=CH_3; R_3=H; R_4,R_5,R_6=CH_3O: O-methyl-pellotine

R_1=H; R_2=CH_3; R_3=H; R_4,R_5=CH_3O; R_6=H: N-methylpellotine

R_1,R_2=CH_3; R_3=H; R_4,R_5=CH_3O; R_6=H: carnegine

R_1=CH_2OH; R_2=CH_3; R_3=OH; R_4,R_5=CH_3O; R_6=H: deglucopterocereine



backebergine

FIGURE 25. Alkaloids isolated from columnar cactus stems (Tables 2 and 3).

problematic, although on morphological grounds *Carnegiea* is most similar to *Neobuxbaumia euphorbioides* (Haw.) Buxb., which appears to lack alkaloids entirely.

Phylogenetic conclusions on Pachycereeae. The theme of this paper has been that systematic treatments of cacti have been in a constant state of flux since Linnaeus first assigned them Latin binomials. With each additional data set, interspecific relationships have been reanalyzed and taxa readjusted to achieve a more parsimonious phylogenetic model. Instead of relying only on gross, external morphological features to reconstruct phylogenies, workers have had to use more subtle or hidden synapomorphic features, such as characters of stem anatomy, seed ultrastructure, areolar and funicular pigmentation, and stem chemistry, to uncover genealogical relationships of the species. Phylogenetic hypotheses generated by combining new and subtle parameters with traditional and conspicuous features are producing a new classification of the large columnar cacti of Mexico, which can be used to study patterns of speciation in the Pachycereeae and to stabilize nomenclature.

Some aspects of the phylogenetic studies of Pachycereeae are still unresolved, in part because morphological, anatomical, and chemical data are incomplete on species residing in southernmost Mexico, and in part because we seem to be running out of "easy" synapomorphies to use in discerning cladogenesis in some of the species groups. For example, to use triterpene and flavonoid data for phylogenetic reconstruction of Stenocereinae, a massive project would be needed to identify each glycosidic compound in sample populations of every species, and this project is not a trivial one because these species have 50–100 distinct compounds per sample.

Tribe Pachycereeae has not yet been defined as a true monophyletic clade, because there is no way to determine at this time with our insufficient data base whether taxa currently classified in other tribes should be brought into Pachycereeae and whether other taxa, such as some of the remnants of *Lemaireocereus,* are part of Pachycereeae. For example, one current problem is *L. aragonii* Britt. & Rose, which grows in dry tropical deciduous forest and disturbed habitats in western Costa Rica. Like *Pachycereus marginatus,* this species can be used as a living fence because its young, unbranched stems root very easily; in addition, this Costa Rican taxon does not appear to produce flowers and fruits very often. Britton and Rose (1919–1923) presented a very incomplete diagnosis of *L. aragonii,* but they were impressed by the wax chevrons produced on young stems marking growth intervals. The seeds of this species were described as shiny,

black, and 3 mm long, features not expected in Stenocereinae but more similar to *Pachycereus.* However, stem materials collected in Costa Rica by M. E. Mathias were examined and found to have none of the characteristic features of either taxon, and they do not blacken when cut. If *L. aragonii* is a species of *Armatocereus,* which it might be, then extensive studies of that genus are required, and then a study of columnar forms must be extended to northern South America. Moreover, this species is the type of *Marshallocereus* Backeb., which included *Stenocereus thurberi,* so additional nomenclatural problems may have to be resolved.

Searching for outgroups to produce a convincing model of Pachycereeae is also not a trivial matter. The normal procedure for studying phylogenetic systematics is to know the limits of the taxon and probable outgroups *before* analyzing infrataxon relationships. Certainly, this cannot be done in cacti without strongly biasing analyses, and it is safer to start reconstructing the phylogenies of tight species groups and work gradually to higher taxonomic levels. Using Stenocereinae as a model, we can see how this can be accomplished, assuming that all species have been included and making informed decisions on where generic lines should be drawn. For example, in Stenocereinae, *Escontria, Myrtillocactus, Polaskia,* and *Stenocereus* are defensible genera because they are each sharply defined by several to many structural and chemical synapomorphies, and each is as distinct as many well-defined genera in other tribes of Cactoideae. For these same reasons, it makes no sense to continue to use the name *Cereus* for any native columnar cactus from Mexico, because *Cereus* s.s. is as distinctive in its own way and has not been ancestral to either Stenocereinae or Pachycereinae.

The problems of developing a parsimonious phylogenetic model of cacti are not insurmountable if workers begin to abandon earlier treatments and reanalyze synapomorphies. An example of this is the epiphytes, which have been another longstanding systematic conundrum. The most recent generic classification of cacti by Hunt (1967) placed all epiphytic genera in one tribe, Hylocereeae Buxb., which included the terrestrial genus *Selenicereus* Britt. & Rose. This treatment is unsatisfactory for three important reasons. First, the primarily South American rhipsalid genera appear to be most closely related to *Corryocactus* Britt. & Rose (incl. *Erdisia* Britt. & Rose; tribe Notocacteae Buxb.), and cannot be related to the ribbed epiphytes of Mesoamerica. Second, even among the epiphytic genera centered around Mesoamerica, there seem to be three clades, and each of these epiphytic lineages is most closely related to a different terrestrial genus, *Selenicereus, Acanthocereus* (A. Berger) Britt. & Rose, or *Nyctocereus* (A. Berger) Britt. & Rose. Therefore, epiphytism has apparently evolved independently in the family at least four times. Finally, if epiphytes have evolved repeatedly from terrestrial forms, then a phylogenetic classification must place terrestrial and epiphytic sister groups in the same taxon. This is the future direction that cactus systematics must take so that the evolutionary history of this family can be properly studied.

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YUCCAS AND YUCCA MOTHS—A HISTORICAL COMMENTARY[1]

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ABSTRACT

The famous yucca–yucca moth pollination mutualism is presented in simplified, idealized form in most biology text books and some books on pollination biology itself. In fact, the interaction is probably more complicated than any single account has implied. It was first noticed in 1872 by George Engelmann but worked on much more by entomologist C. V. Riley and botanist W. Trelease. A conventional statement of the sequence of events is given and the complications are considered. References to seed setting in the absence of *Tegeticula* are reported that may be due to self-pollination or to the activities of other flower visitors. A nectar reward is provided by septal nectaries at the base of the ovary in many species of *Yucca*. There is disagreement among authors as to whether plants of some species are self-compatible and as to the extent of geitonogamy in various species. *Tegeticula yuccasella* appears to be the pollinator of all yucca species east of the Rockies and all the western species except *Yucca whipplei* (sensu lato) and *Y. brevifolia*. *Yucca whipplei* is served by *Tegeticula maculata*, which is diurnal in operation and has to contend with a capitate stigma. *Yucca brevifolia* also has its own species of yucca moth (*T. synthetica*). Natural hybridization appears to be rampant in the species pollinated by *T. yuccasella* but not for the two western species that have separate *Tegeticula* pollinators. There is some evidence, however, that *T. yuccasella* is a complex of taxa separately adapted to individual species of *Yucca*. Another genus is concerned with the pollination in Arizona and southeastern Mexico: *Parategeticula*, which has very different oviposition and larval behavior. "Tentacleless" *Tegeticula* occur in significant proportions in some populations and, like the "bogus yucca moths," they are purely parasitic, not displaying any pollinatory activities. An attempt at placing these organisms in an evolutionary context is made.

It is interesting that in pollination biology and other disciplines significant biological discoveries become increasingly simplified in the telling and retelling of the story in text books and the general biological literature, even as the actual process is discovered to be increasingly complex. Thus, the pollination biology of the 35 or 40 species of *Yucca* is widely quoted as a unique example of strict mutualism—the yucca being entirely dependent on the yucca moth for pollination and the moth being totally dependent on some of the developing yucca seeds for the nourishment of its larvae.

The relation of the yucca moth to the yucca plant has especial relevance to us in that it was first seen by the man honored by this symposium—Dr. George Engelmann. Notes on file at the Missouri Botanical Garden referring to the pollination of yucca plants include those made by Dr. Engelmann in 1872.

1872. June 13th . . . .

I see many insects about the flowers, bees bumblebees and others, but principally a white moth of the alliance of *Tortrix* [crossed out] *Tinea* often two (a pair!) in one flower, which fly at dusk, but are quickly [?] hid in the flower in day time.

They seem to transport the pollen into the stigmatic tube . . . .

July 16th. Capsules very much constricted, remain small, none full grown. Today [I] observed the first holes in them, where a larva of our [?] moth has gnawed through and escaped (into the ground?). Opening a capsule I find 4 or more larvae in it and almost all the seeds eaten up.

In the first days of July *Mr Riley* found the Yucca in full bloom in Kirkwood [Missouri], fertilized by the moth—which by a peculiar appendage of the mandible (peculiar to the female, wanting in the male) gathers up the pollen, pushes it into the stigmatic tube and lays its egg (into it-no). [Parentheses and "no" added later in pencil.]

In the Bulletin of the Torrey Botanical Club for July 1872, Engelmann (1872a) reported the

[1] I am grateful to B. L. Mykrantz, archivist at the Missouri Botanical Garden, for photocopies of correspondence by Engelmann and Riley, and to G. Davidse for inviting me to contribute to the symposium and for much help with logistics. I thank J. Powell for much good advice and the use of his photograph of *Tegeticula*, D. Davis for giving permission to reproduce his drawing of *Parategeticula*, and L. Heckard for permission to use photographs in the Jepson Herbarium collection at U.C. Berkeley. Irene Baker assisted in every possible way.

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pollination of yucca flowers by a white moth of the genus *Tortrix*. Subsequently, he protested that he had written "allied to *Tortrix*" (Engelmann, 1872b).

But it was Dr. Charles V. Riley, the Missouri State Entomologist, who worked for over 20 years on the pollination biology and systematics of the moths involved and their relatives, continuing the work he began in Missouri when he became Chief of the Entomology Division of the U.S. Department of Agriculture. His first account was delivered at a meeting of the American Association for the Advancement of Science at Dubuque, Iowa, which was picked up by the British journal "Nature" in August 1872 (Anon., 1872). Riley wrote many papers on the mutualism (e.g., Riley, 1872, 1881, 1892, 1893). A full listing of Riley's papers is given by Davis (1967). Contributions were also made by Dr. William Trelease, Director of the Missouri Botanical Garden (Trelease, 1893, 1902). Coquillet (1893) observed the pollination of *Yucca whipplei* in California. In the older references the moth genus is given as *Pronuba*, but that name was shown to be invalid and has been replaced by *Tegeticula* (Davis, 1967).

Yucca–Yucca Moth Mutualism

What is the marvellous story as described by Riley?

The female moth emerges from a pupa in the ground near a yucca plant and mates in the yucca flower with a male (who plays no part in the pollination process). She (Fig. 1) flies nocturnally to a freshly opened *Yucca* flower and with specially adapted mouthparts (including "tentacles" on the maxillae, Fig. 2), scrapes pollen from the anthers and forms it into a ball that she carries between the "tentacles" and her thorax (Fig. 3).

Then she supposedly flies to another plant and, finding a suitably receptive flower, she enters it and, aligning herself appropriately, with her ovipositor she penetrates the ovary wall and lays a thread-like egg in one of the locules in the superior ovary. Then she clambers from the base of the flower (actually often uppermost because the flowers are frequently pendulous) to a position from which she can place some or all of her pollen load in the tube that is formed by the separated ends of the fused styles (Fig. 4). She rams the pollen into this stigmatic groove (which is lined with papillae and exudes a stigmatic exudate). Pollen could not easily get there without the aid that she gives it. But the yucca moth does not feed at all.

There may be repeat performances of egg-laying by the moth so that several locules of the ovary will receive eggs. But, with the pollination achieved, the food supply of the larva (the developing seeds) is assured, while not all of the seeds are destroyed and the survivors are available to perpetuate the yucca species.

There are six locules in the ovary and each may receive one or more eggs. The larvae consume seeds in their immediate vicinity and the fruit shows a constriction in the region of a larva. The larva bites a hole in the fruit wall when it reaches the right state of maturity and descends to the ground either on a silken thread (Riley, 1892) or more likely simply by dropping (Davis, 1967). Entering the soil it forms a cocoon and rests until an environmental signal causes it to pupate and shortly afterwards, the adult emerges and the stage is set for the annual re-enactment of the interaction. The timing of the emergence is closely correlated with the flowering of the yucca.

Correspondence on file at the Missouri Botanical Garden indicates that Riley sent cocoons of *T. yuccasella* to at least five persons in charge of ornamental yucca plantings in Europe and in Massachusetts, where the moth does not occur naturally, to see if the moths would emerge and pollinate these yuccas. Unfortunately, we do not know if they were successful experiments. Possibly the timing of emergence would not be correct in the new environments.

Galil (1973) has suggested that the apparently purposeful pollinatory activity of the yucca moth deserves recognition as "ethodynamic" pollination as opposed to the conventional "topocentric" pollination (depending upon the relative positions of anthers and stigma, with pollination clearly mechanical). Only *Ficus* provides other known cases of ethodynamic pollination.

Complications

In the text books this story is held to be a valid generalization for all yuccas and yucca moths. But careful reading of first-hand accounts that have been published reveals that the true situation may be more complicated. Some field reports suggest that other potential pollinators visit *Yucca* and further, seed set may occur without pollinator intervention.

Wiggins (1980: 834), in his flora of Baja Cal-

FIGURES 1–4.—1. Female yucca moth (*Tegeticula synthetica*) in flower of *Yucca brevifolia*. Photo by C. S. Webber in the Jepson Herbarium, University of California, Berkeley.—2. Side view of head of yucca moth (*T. synthetica*) showing one maxillary palpus (mp) with its "tentacle" (mt) as well as the base of the antenna (at), eye (e), front trochanter (ft), labial palpus (lp), bristle (b), and proboscis (t). From Riley (1892).—3. Female yucca moth (*T. maculata*) with ball of pollen. Photo by J. Powell.—4. Half flower of *Yucca brevifolia* showing carpels separated at apex, producing the stigmatic groove. Photo by C. S. Webber in the Jepson Herbarium, U.C.B.

ifornia, noted that "All of the yucca species are attractive plants. Their flowers are delicately fragrant and attract bees, wasps, moths and beetles." But we do not know which of these are effective pollinators. It is frequently stated that the yucca has no possible pollinators besides the yucca moth, although reports of seed-setting by yuccas not serviced by yucca moths appeared as early as 1892 in a note to the Torrey Botanical Club by "J.W.B." of Flushing, Long Island (probably J. W. Barstow), who mentioned that "In my own garden, the *Y. filamentosa* Gray, blooms and matures its seed annually. I have never been able to discover the intervention of any insect to assist fertilization, nor have I ever failed to secure the prompt germination of seed taken from any well-matured capsule." The same species, *Yucca filamentosa,* was cultivated in Israel by Jacob Galil. He reported (Galil, 1973) that "In *Y. filamentosa* spontaneous fruit set is never encountered in the garden" but Galil did find this to occur in *Yucca aloifolia,* which was also cultivated there. This he attributed to the action of honey bees. He is one of the few authors who have drawn attention to the fact that most yuccas have some nectar secretion from septal nectaries on the ovary. This may be quite voluminous in some species (e.g., *Y. guatemalensis* and *Y. elata,* Trelease, 1893).

There is also a more or less abundant stigmatic secretion that could serve as a reward to flower-visitors as it contains sugars (Horowitz et al., 1972). It is most abundant in *Yucca aloifolia.* In Israel, Galil (1973) pointed out that cultivated plants of both *Y. aloifolia* and *Y. filamentosa* are self-compatible, in contrast to the conclusion by East (1940) that these species are self-incompatible. Trelease (1893) also referred to the frequent fruiting of *Y. aloifolia* without *Tegeticula* pollination.

TABLE 1. Infra-generic classification of Yucca (35–49 spp.).

I	SARCOCARPA	fleshy fruit; lobed stigma	a number of spp.
II	CLISTOCARPA	spongy fruit; lobed stigma	*Y. brevifolia*
III	HESPEROYUCCA	dehiscent capsule; capitate stigma	*Y. whipplei* (s.l.)
IV	CHAENOCARPA	dehiscent capsule; lobed stigma	a number of spp.

"Spontaneous" seed-setting was also found by Webber (1953) in *Yucca whipplei* and, at least, self-compatibility (though not necessarily self-pollination) in some populations of this species has been commented upon by several other authors (e.g., McKelvey, 1947; Wimber, 1958; Powell & Mackie, 1966; Aker, 1981, 1982a, 1982b). These authors concluded that self-pollination in this species was uncommon. Webber (1953: 67), based on years of collecting and observing yuccas in the southwestern states, wrote:

> Outside of *Y. brevifolia* and *Y. whipplei,* our southwestern yuccas are not reproducing to any extent by seeds. There can be little question, therefore, that the yucca moth is more dependent on the yucca for its existence than the yucca is on the moth. During their long life, through vegetative reproduction, the majority of yuccas would continue to exist for many years without the moth. On the other hand, it appears that the yucca moth would be completely wiped out if the yuccas failed to flower for a single year.
>
> Regardless of the fact that yuccas are about equally self- and cross-fertile and that the moth flies from flower to flower, it is doubtful if cross-pollinations are as prevalent as reported. It is very likely that the number of self-pollinated flowers far exceeds the number of cross-pollinated ones, and except in areas where species are admixed and flower at the same time interspecific crossing is but remotely possible.

This view is possibly too extreme but the situation does require further study. Apparently, Webber was not correct in assuming that all the moths in the soil would emerge the next year. Aker (1981, 1982a) pointed out that the emergence may be spread over three years.

A Plurality of Yucca Moths

Botanists too easily refer to insects by all-inclusive names—like "the bee" and "the ant." So it is with *the* yucca moth. Actually, there are at least four species of pollinating yucca moth (and even two genera). Thus, *Tegeticula yuccasella* seems to be the pollinator of all the *Yucca* species east of the Rocky Mountains and of all the western species except *Yucca whipplei* (in the wide sense) and *Yucca brevifolia,* which have their own species of *Tegeticula* (McKelvey, 1938, 1947). This fits with the generally accepted systematics of the genus *Yucca* (Trelease, 1902) where four sections are recognized if the genus is not split (Table 1).

Yucca whipplei is so different in several morphological, physiological, and ecological features that it has been suggested that a separate genus *Hesperoyucca* be set up to accommodate it (J. G. Baker, 1892). Consequently, it is not surprising that it has a separate species of yucca moth, *Tegeticula maculata* (Table 2), which can operate in the daytime and which has to smear pollen (which is stickier than in other yuccas) on a capitate stigma instead of ramming it into a stigmatic groove (Fig. 5). Several twentieth century studies of the pollination of *Yucca whipplei* have been made (McKelvey, 1947; Webber, 1953; Wimber, 1958; Powell & Mackie, 1966; Udovic, 1981; Aker, 1981, 1982a, 1982b; Udovic & Aker, 1981; Aker & Udovic, 1981) and its pollination biology is probably better known than that of any other species of *Yucca.*

Yucca whipplei, including *Y. peninsularis* and *Y. newberryi,* has at least six morphologically distinct subspecies (Haines, 1941; Epling & Haines, 1957). Its *Tegeticula* (*T. maculata*) has a melanic subspecies (subsp. *extranea*) as well as the type subspecies (subsp. *maculata*).

Yucca brevifolia, the Joshua tree, is the only species with a "papery" or "spongy" fruit. It has a yucca moth, *Tegeticula synthetica* (also known as *T. paradoxa*) entirely to itself (Table 2) (McKelvey, 1947; Davis, 1967).

Timing and Moth Emergence

Powell and Mackie (1966) showed that *Yucca whipplei* flowers may be available for two to three months, so precise timing of the emergence of the moth is not essential for this species. However, in other species this does seem to be precise

TABLE 2. *Tegeticula* species associated with sections of the genus *Yucca*.

SARCOCARPA, CHAENOCARPA	*Tegeticula yuccasella*
CLISTOCARPA	*Tegeticula synthetica*
HESPEROYUCCA	*Tegeticula maculata*

and Rau (1945), who made sustained observations at Kirkwood (the place in Missouri where the mutualism was first investigated) found evidence that temperature was an important controlling factor in the coincidence of flowering of *Yucca filamentosa* and the emergence of the moth. For *Yucca whipplei,* Powell and Mackie (1966) suggested that the rainfall pattern is crucial.

HYBRIDIZATION AND SYSTEMATICS

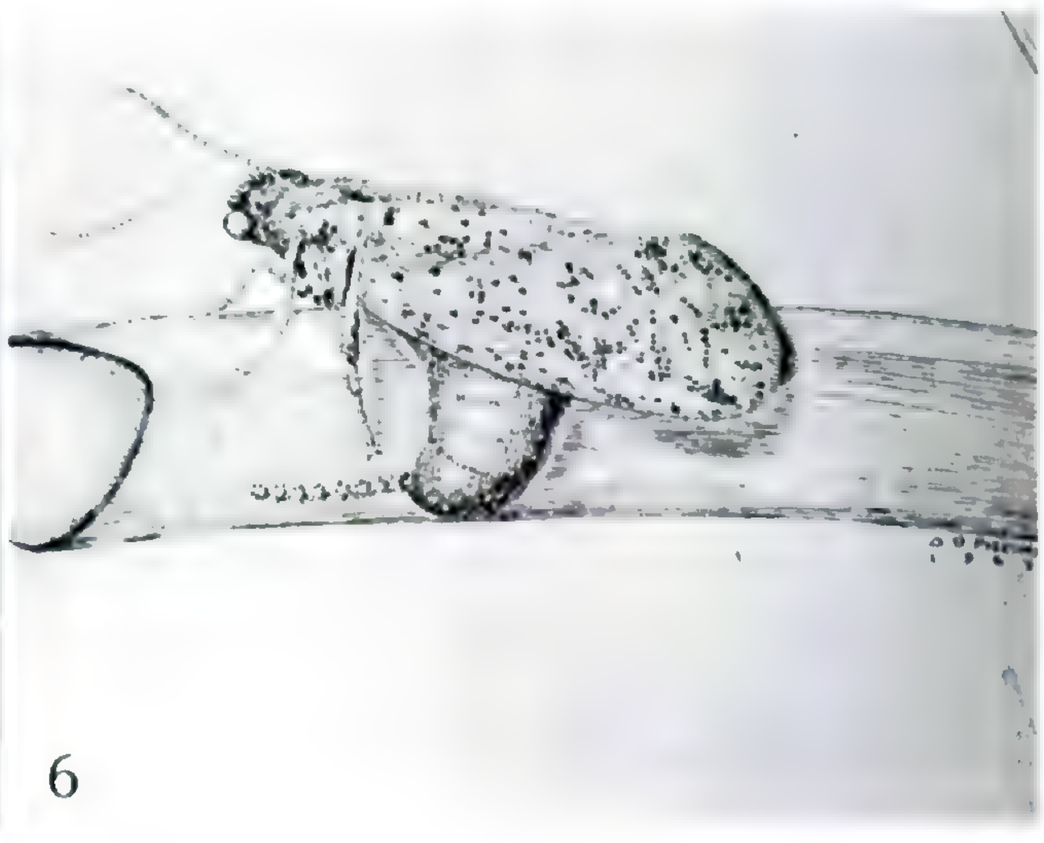
It is notable that interspecific hybridization is rampant among the species that are pollinated by *Tegeticula yuccasella.* Webber (1953) listed at least 15 combinations, and McKelvey (1938, 1947) found others. Webber (1953) and Galil (1973) have both obtained seed from artificial crosses. The gene-flow in nature may be responsible for the blurred specific boundaries between some of the species and taxonomic disagreements about species limits. But the two yucca species that have their own yucca moth species have remained free from hybridization, even where they have come into proximity to other species.

Nevertheless, there is evidence that *Tegeticula yuccasella* is not an indivisible unit systematically and ecologically. Davis (1967) seems to have been the first to suggest that all *Tegeticula yuccasella* are not alike. Particularly the variation in genitalia suggested to him that there might be distinct yucca moths associated with each of the four sections of the genus *Yucca.* We know that *Yucca brevifolia* has its own *Tegeticula,* as does *Y. whipplei*; what he suggested is that there are also distinct moths for the sections *Sarcocarpa* and *Chaenocarpa.*

In 1983, Miles carried the process further and suggested that on the basis of morphological and phenological characters shown by the moths that pollinate *Yucca baccata* and *Yucca torreyi* (section *Sarcocarpa*) and *Yucca elata* (section *Chaenocarpa*) in New Mexico, there are separate moth entities in each case, although all had been put in *Tegeticula yuccasella* in previous work. She hinted at the possibility that each yucca species has its own pollinating moth. But, I think that, in view of the widespread hybridization and blurring of specific characters in yucca east of the Rockies, the differentiation of the moths must be only at the race level rather than at the species level, with the opportunity for "mistakes" to occur with the moths pollinating taxonomically different plants than the kind that produced them. Thus, Miles (1983) found some evidence of the use of *Yucca torreyi* by moths of the *Yucca baccata* form when *Y. baccata* had finished blooming.

PARATEGETICULA

I think it will come as a shock to most people that there is another genus of moth that polli-



FIGURES 5, 6.—5. Half flower of *Yucca whipplei,* with capitate, papillate-fringed stigma. Photo by C. S. Webber in the Jepson Herbarium, U.C.B.—6. Oviposition by *Parategeticula pollenifera* on pedicel of *Y. schottii.* From Davis (1967).

nates yucca, although it was described 17 years ago by Davis (1967). It was news to me when I began to assemble information for this paper, and none of the general pollination accounts published so far mention it.

The new genus is *Parategeticula* and the only species known is *P. pollenifera* (Fig. 6). It was first collected in 1959, in southeastern Arizona and subsequently, a long way away, in Veracruz, in southeastern Mexico in 1963. Davis, whose monograph on the subfamily Prodoxidae is the standard reference (Davis, 1967), went to Arizona to see it in the flowers of *Yucca schottii.* Powell (1985) has subsequently made a detailed study of this moth both in Arizona and in Veracruz (where he found it in *Yucca elephantipes*).

Parategeticula females have "tentacles" like *Tegeticula* and gather up pollen in a ball in the same fashion. Neither Davis nor Powell was able to see that it pollinated the stigma by actively pushing the pollen into the stigmatic cavity, but it seems reasonable to expect that it does.

Parategeticula then does a surprising thing. Instead of ovipositing in the ovary of the flower, it sometimes lays eggs in the fleshy petals or else in a carefully gouged line of shallow pits on the flower stalks (Fig. 6). Davis (1967) thought that it would not cause any loss of seeds to the yucca by having its larvae feed in the stem tissue, but Powell (1985) found that after development from the egg, the larva crawls up to the developing ovary and bites a hole to let itself in.

In the ovary, the larva causes degradation of the tissues of the inner side of the wall and the adjacent ovules. In the cyst that is formed, the larva then eats the distintegrated ovules. This unique larval behavior is very different from that of *Tegeticula* whose larvae develop from eggs in the ovary and wait there until the seeds are almost ripe before consuming them.

Populations of *Yucca schottii* in Arizona may have only *Tegeticula yuccasella* or only *Parategeticula pollenifera* or both at the same time (Powell, 1985). Obviously, *Parategeticula* must be looked for in more species of yucca, especially in the gap between Arizona and Veracruz.

Allogamy or Geitonogamy?

It is very important to know the breeding systems of the various *Yucca* species. It seems, from the experiments of East (1940), Webber (1953), Wimber (1958), Udovic and Aker (1981), Aker (1981, 1982a, 1982b) that at least some plants of *Yucca whipplei* are self-incompatible and Webber found some self-incompatibility in six other species. Consequently, some authors have tended to take for granted that the female yucca moth regularly flies between separate plants before depositing her pollen load.

Jepson (1925: 246) wrote "The female Pronuba works by night, collecting the pollen from the anthers and rolling it into a little ball: she then flies to the flower of another plant, deposits her eggs in the ovary, and then in a manner which corresponds to actions full of purpose and deliberation climbs to the style and thrusts the pollen ball down the stigmatic tube." There is no evidence that Jepson actually saw this at first hand; the vehicle of publication being a California flora. In fact, none of the first-hand accounts justify this categorical statement that another plant is immediately sought by the *Tegeticula* moth after collecting the pollen ball.

Riley (1892) wrote "After collecting all the pollen . . . she *usually* runs about or flies to another plant; for I have often noticed that oviposition, as a rule, is accomplished in some other flower than that from which the pollen was gathered, and that cross-fertilization is thus secured" [emphasis added]. It is not clear whether the "other flower" in this quotation is more frequently in the same inflorescence than in another plant.

Trelease (in Riley, 1892: 125) wrote "Apropos of Meehan's idea that the Pronuba moth close fertilizes the flower, I have seen females when undisturbed *go from flower to flower here,* and several times in the mountains a female was seen, without having been disturbed, to fly off horizontally from a plant on the steep mountain side, with every evidence of the necessity for a long flight before finding another Yucca" [emphasis added]. This does not necessarily imply that the horizontal flight led to cross-pollination.

Webber (1953) has already been quoted as holding the opinion that more selfings take place than outcrossings. Rau (1945: 374) wrote "The moth, when ready to oviposit, gathers a ball of the sticky pollen from the anthers . . . holding it firmly under her chin she *runs* about until she finds a flower which is suitable for ovipositing" [emphasis added].

There must be inter-plant flights by the moths; the interspecific hybrids testify to this, but the evidence is circumstantial. The nearest direct evidence is provided by Aker and Udovic (1981) in the case of *Tegeticula maculata* on *Yucca whipplei,* which is easier to observe because the

activity is in daylight rather than nocturnal. They wrote "In no case was a female seen ovipositing in the same inflorescence after collecting pollen. Having collected a full load of pollen the females typically crawl out on the branches or unopened flower buds, rest briefly and then fly off. In those cases where it was possible to observe them in flight, they either flew away in a straight line if there was no obstacle, or else spiralled out from the inflorescence until they were heading down wind and then flew straight. The flights were generally high, well above the surrounding vegetation, and the moths often ignored other inflorescences nearby" (Aker & Udovic, 1981: 96).

Furthermore, Aker and Udovic (1981: 97) stated "—the fact that dispersing females fly relatively long distances (i.e. tens of meters) suggests that they are minimizing the likelihood that they will return to the same plant from which they have collected pollen or visit other closely related individuals in the vicinity of the pollen donor."

Powell and Mackie (1966) do not say that they saw *Tegeticula maculata* go from plant to plant of *Yucca whipplei.* However, Powell (1985) has more recently used mark/recapture methods to show that male *Parategeticula* (the other genus) stay on one plant of *Yucca schottii* while the females go to other plants, at least sometimes.

If a plant is self-incompatible, geitonogamy will be worse than useless. Clogging of the stigma by incompatible pollen could be one cause of the tremendous voluntary shedding of fruits in *Yucca,* 50–90% according to Aker (1981, 1982a, 1982b) and Aker and Udovic (1981). They have shown that limited resources are an important cause of this and, in addition, point out that the large numbers of flowers increase the visibility of plants to the moth, and in an exceptionally favorable season there may be a higher proportion of fruits that can mature. All of these factors as well as the geitonogamy possibility may be operative.

PARASITISM DERIVED FROM MUTUALISM

Sometimes, *Tegeticula* oviposits without pollinating. Sometimes it lays eggs in an ovary that is already developing following pollination by a previous visitor (Aker, 1981). In such cases, that particular *Tegeticula* individual is unequivocally parasitic.

This leads us to another complication. It is assumed that all the female *Tegeticula* moths are potentially capable of pollinating the *Yucca* flower but observation of collections and sampling of populations shows that this is not always so (Davis, 1967). An essential item in the pollination system is the presence on the maxillary palpus of the female moth of the "tentacles," which make possible the processing of the pollen into a ball that is carried between the underside of the mouth parts and the thorax of the moth (Figs. 2, 3).

But August Busck, who examined the many collections by Susan McKelvey (see McKelvey, 1947), pointed out that he found "20–30" out of at least a thousand specimens of female *Tegeticula* to have vestigial "tentacles" or none at all. Davis (1967) investigated this in population samples of *Tegeticula yuccasella* and found that the percentage of tentacle-less female moths could vary from zero to 71%. These tentacle-less moths apparently do not attempt to collect pollen, and if they oviposit they constitute parasites on the mutualism. It is clear that if the proportion of non-pollinators grows beyond a certain point the yucca will be less frequently adequately pollinated and it will be interesting if further quantitative analyses are made of this phenomenon and its effect on population structure in *Yucca.*

Keeley et al. (1984) discussed seed predation of nine species of *Yucca,* pointing out that in all these species, although there were some fruits in which all the seeds were consumed and some with only a proportion consumed, there were others in which no larvae were to be found. This could be due to self pollination or pollination by some other agent than *Tegeticula,* or to the failure of the moth to oviposit though it pollinated the flower. Most likely, the moth oviposited but the larvae died. They hint that some *Yucca* populations may be capable of inhibiting the hatching of *Tegeticula* eggs and thus "regulating Tegeticula densities" in their populations. However, at present, this is speculation.

"BOGUS" YUCCA MOTHS

In addition to *Tegeticula* and *Parategeticula,* there are what Riley (1892) called "bogus yucca moths." Three genera are involved. They also are members of the Prodoxidae and oviposit in the wall of the ovary or in some part of the stem system (Powell & Mackie, 1966; Davis, 1967). They have no tentacles, and even if they visit the flowers, they do not collect pollen. Consequently they are dependent for their larval survival on

the pollinating acitvities of *Tegeticula,* which causes the flowers not to be abscised and seed to be set that will result in new *Yucca* plants.

Evolutionary History

What may be the evolutionary sequence in building the yucca–yucca moth mutualism?

In the Agavaceae, apart from *Yucca* species, pollination is topocentric (see page 557), and it is likely that a distant ancestor had this conventional pollination mechanism, which is pointed to by the production of floral nectar. When association with the Prodoxidae began (probably by the greater certainty of pollination by these moths), *Tegeticula* itself may be the starting point—an assumption that is in keeping with the universality of its association with *Yucca* as the virtually exclusive pollinator. We can either postulate that the "bogus yucca moths" evolved from *Tegeticula* with the *Tegeticula* providing the pollination for them, or some other pollinator may have been involved. The "tentacle-less" *Tegeticula* females may represent a mutant form that could show the ancestral condition. Galil (1973) considers the mutualism of *Yucca* and *Tegeticula* to be an evolutionarily rather recent event (basing this on the continued production of "useless" nectar) but the occurrence of the mutualism in all yuccas seems to point to a longer history. This is particularly the case in that *Yucca whipplei* has significant morphological differences from the rest of the genus, yet possesses *Tegeticula,* which has had time to produce subspecies, matching in distribution the subspecies of this yucca that have disjunct populations probably relict from a more continuous distribution at some time in the past (Powell & Mackie, 1966).

Parategeticula could be either derived from *Tegeticula* or ancestral to it. It has a distribution (admittedly not fully revealed as yet) that is within the bounds of *Tegeticula.* But it is hard to see its oviposition behavior and the movements of its larvae making a perilous journey from pedicel to ovary as an advantage over the direct oviposition into the ovary practiced by *Tegeticula* (so it might be more primitive than *Tegeticula*).

As stated above, it is notable that none of the other American genera in the Agavaceae have developed a comparable mutualism; *Agave* has many different pollinators, *Nolina* and *Dasylirion* tend to show separation of the sexes, while *Hesperaloe* may be bird-pollinated.

Possible Parallels

As for the combination of lepidopteran pollinator and seed-predator, the only suggestive case outside of *Yucca* apparently concerns *Silene alba* (also known as *S. pratense* and *S. latifolia*), where both male and female moths of *Hadena bicruris* visit the white flowers at night in Europe (Brantges, 1976). Both staminate and pistillate flowers of this dioecious species are visited for the nectar they produce, and cross-pollination is achieved. But the female moth oviposits on the ovary in pistillate flowers and the larva eats its way into the ovary and consumes the seeds. It then moves to other flowers on the plant and consumes their seeds before descending to the ground and pupating.

Brantges (1976) has calculated that the larvae consume the contents of as many fruits as the moths had pollinated, and it is only because other non-seed predatory moths also pollinate *Silene alba* that it produces enough seed to reproduce itself (it is an annual plant). It is possible that *Silene alba* may evolve some means of curbing the appetite of the larva, in which case a mutualism of the yucca sort might be possible, but this is highly speculatory.

The simple story of mutualism between a flower and an insect is probably basically sound, but the situations in nature are being revealed to be more complex than George Engelmann had any reason to anticipate and it is to be hoped that research (observational and experimental) into this fascinating area will be stimulated by the need for more information.

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CENOZOIC HISTORY OF SOME WESTERN AMERICAN PINES[1]

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ABSTRACT

Since *Pinus* occurs in the Early Cretaceous (ca. 125–130 Ma), it probably had emerged from a *Pityostrobus* complex by the Late Jurassic (ca. 140–135 Ma). Initial adaptation to seasonal climate and drier sites may account for rapid evolution on several occasions. This presumably was enhanced by symbiotic association with ectotrophic mycorrhizae that gave pines an adaptive advantage in new, spreading, more stressful environments throughout its history. *Pinus* probably underwent major splitting into early subsections in the Late Cretaceous-Early Tertiary as Laramide tectonism created new environments (dry slopes, rain shadows). In the later Eocene-Oligocene, new opportunities for speciation resulted from increased tectonism, volcanism, and the spread of regional dry climate. New drier sites appeared in the Late Oligocene (28–27 Ma) as erosion increased in response to lowered base level as sea level decreased and as Drakes Passage opened and cold water was shunted northward. Further speciation no doubt occurred as seasonally dry climates spread in response to developing ice sheets (East Antarctic, 13 Ma; West Antarctic, 7–6 Ma; Arctic, 4–3 Ma). Continued volcanism, tectonism, and markedly fluctuating climate at the close of the Cenozoic fostered further speciation, especially in Mexico where pines show much intergradation owing to rampant hybridization in the recent past. Species of three subsections (*Cembrae, Strobi, Sylvestres*) in North America are represented by taxa in Eurasia. They reflect the early spread of ancestral taxa into both land areas via connections across the mid-to-north Atlantic and Beringian areas. Neogene records in Europe of taxa allied to east American pines (*Australes*) may be valid but need reevaluation. The fossil record suggests that six of the eight subsections indigenous to North America (*Balfourianae, Cembroides, Leiophyllae, Oocarpae, Ponderosae, Sabinianae*) probably originated over the Cordilleran region that extends southward into Mexico. Subsect. *Australes* may be largely southeastern and the *Contortae* evidently spread northward (*P. contorta, P. banksiana*) and into mountains as colder environments appeared there. Movement along the San Andreas rift system probably transported taxa northward from western Mexico, as indicated by species of *Oocarpae, Leiophyllae,* and *Strobi* in Tertiary rocks of coastal California. As more extreme climates spread in the late Cenozoic, the richer Tertiary forests and woodlands lost taxa, and the survivors retreated to moister areas. Pines now increased numerically as competition was reduced and more space appeared in the impoverished, surviving vegetation zones. In addition, spreading new regional environments, notably drier lowlands (for piñons), drier upland slopes (for *P. ponderosa, P. scopulorum, P. jeffreyi, P. flexilis*), colder, wetter basins (for *P. banksiana, P. contorta*), and cold uplands (for *P. albicaulis, P. aristata, P. contorta, P. monticola*), now became available as more continental climates spread. Pines in these more extreme environments, where they are also associated with ectotrophic mycorrhizae, may form regionally extensive, pure stands. These are not recorded in presently-known Tertiary floras in which pines were members of rich, mixed conifer, conifer hardwood, and sclerophyllous woodland vegetation. During the past few centuries, some pines greatly increased in number as man upset ecosystems by fire, logging, and clearing.

PART 1. HISTORY

Fossil records of Pinaceae are rare in most Cretaceous to early Paleogene rocks. This is because they lived chiefly in sites well removed from the lowland broadleaved forests adapted to warm temperate to tropical, essentially aseasonal, climates of ample rainfall. These conditions were the result of low, widely-flooded continents, the lack of high mountain chains and plateaus,

[1] Many of the fossil pines on which this paper is based were secured by me during the collection of Tertiary floras over the past 50 years. This was made possible by grants from the Carnegie Institution of Washington (1935–1952), the National Science Foundation (1954–), and, intermittently, by the Committees on Research, University of California, Los Angeles and Davis campuses. Acknowledgment is due W. B. Critchfield for permission to compare the remains of fossil pines with the large, excellent collection of modern pines at the Institute of Forest Genetics, Placerville, California. Thanks are also extended to F. M. Hueber, Smithsonian Institution and to J. W. Hall, University of Minnesota, for the loan of critical pine fossils described in earlier reports. In addition, Ruth A. Kirkby, Director of the Jurupa Mountains Cultural Center, Riverside, California, generously granted me permission to study and photograph specimens of *Pinus lindgrenii* Knowlton that she collected in the type area near Bruneau, southern Idaho. The photographs of many of the fossils were taken by Howard Schorn, Dept. Paleontology, University of California, Berkeley. W. B. Critchfield, J. R. Haller, C. Millar, C. N. Miller, Jr., and P. H. Raven reviewed the manuscript and have offered a number of valuable suggestions that have improved it.

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TABLE 1. Subdivisions of genus *Pinus* (after Little & Critchfield, 1969).

		Number of Species	
		*North America	Eurasia
Pinus			
Subgenus 1. DUCAMPOPINUS			
Sect. 1. *Ducamptopinus*		—	1
Subsect. 1. *Krempfianae*			
Subgenus STROBUS			
Sect. 2. *Strobus*			
Subsect. 2. *Cembrae*		1	4
P. albicaulis Engelm.			
3. *Strobi*		6	8
P. ayacahuite Ehrenb.	*P. monticola* Dougl.		
flexilis James	*strobiformis* Engelm.		
lambertiana Dougl.	*strobus* L.		
Sect. 3. *Parrya*			
Subsect. 4. *Cembroides*		8	—
P. cembroides Zucc.	*P. monophylla* Torr. & Fremont		
culminicola Andres. & Beaman	*nelsonii* Shaw		
edulis Engelm.	*pinceana* Gord.		
maximartinezii Rzedow.	*quadrifolia* Parl.		
5. *Gerardianae*		—	2
6. *Balfourianae*		3	—
P. aristata Engelm.			
balfouriana Grev. & Balf.			
longaeva Bailey			
Subgenus PINUS			
Sect. *Ternatae*			
Subsect. 7. *Leiophyllae*		2	—
P. leiophylla Scheide & Deppe			
lumholtzii Robins. & Fern.			
8. *Canarienses*		—	2
9. *Pineae*		—	1
Sect. 5. *Pinus*			
Subsect. 10. *Sylvestres*		2	17
P. resinosa Ait.			
tropicalis Morelet			
11. *Australes*		11	—
P. caribaea Morelet	*P. occidentalis* Sw.		
cubensis Griseb.	*palustris* Mill.		
echinata Mill.	*pungens* Lamb.		
elliottii Engelm.	*rigida* Mill.		
glabra Walt.	*serotina* Michx.		
	taeda L.		
12. *Ponderosae*		14	—
P. arizonica C. E. Blanco	*P. michoacana* Martinez		
douglasiana Martinez	*montezumae* Lamb.		
durangensis Martinez	*ponderosa* Laws.		
engelmannii Carr.	*pseudostrobus* Lindl.		
hartwegii Lindl.	*teocote* Scheide & Deppe		
jeffreyi Grev. & Balf.	*washoensis* Mason & Stockwell		
lawsonii Roezl			

TABLE 1. Continued.

		Number of Species	
		*North America	Eurasia
13. *Sabinianae*		3	—
P. coulteri D. Don			
sabiniana Dougl.			
torreyana Parry			
14. *Contortae*		4	—
P. banksiana Lamb.	*P. contorta* Dougl.		
clausa (Chapm.) Vasey	*virginiana* Mill.		
15. *Oocarpae*		8	—
P. attenuata Lemm.	*P. patula* Schiede & Deppe		
greggii Engelm.	*pringlei* Shaw		
muricata D. Don	*radiata* D. Don		
oocarpa Schiede	*remorata* Mason		
	Totals	62	35

* Names of American species only are listed here; from Little and Critchfield, 1969, plus *P. remorata* in *Oocarpae*.

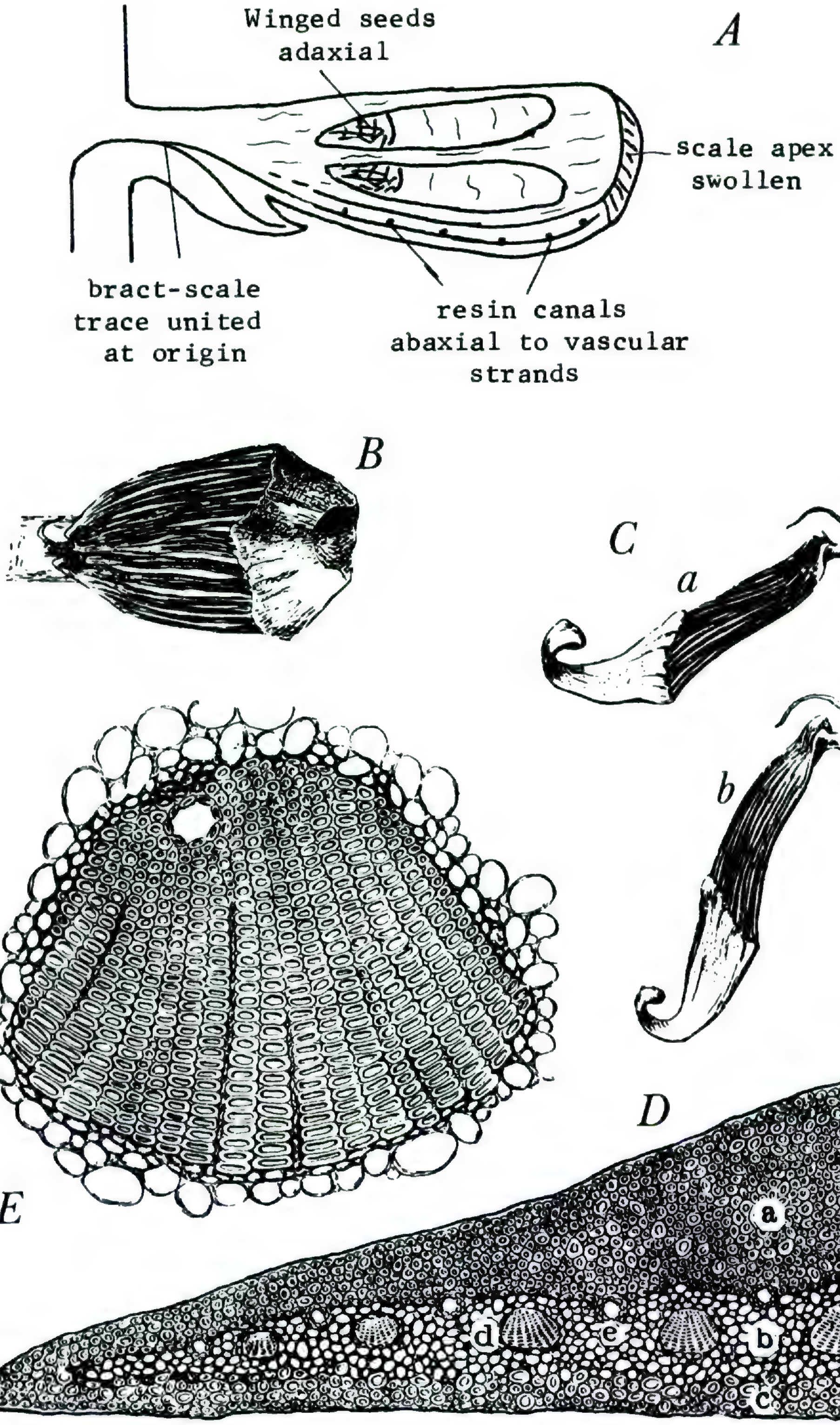
and the absence of polar ice caps. By contrast, Pinaceae, and *Pinus* in particular, adapted early to seasonal climates. This is apparent from the records of relatively abundant Pinaceae (*Abies, Picea, Pinus, Pseudotsuga, Tsuga*) in the few montane floras that are known. Examples include the Princeton flora, British Columbia (Arnold, 1955; Miller, 1973; Stockey, 1984), the Copper Basin (Axelrod, 1966a) and Bull Run floras (in Axelrod, 1968, MS), northeastern Nevada, and the Florissant (MacGinitie, 1953) and Creede (Knowlton, 1923; Axelrod, unpubl. data) of Colorado. The Paleogene floras of arctic and subarctic regions also have remains of Pinaceae, including *Pinus* (Heer, 1868–1883). In view of these circumstances, we know relatively little of the initial history of *Pinus*. The earliest records of presumed pine-like taxa (see Miller, 1977a) include needles and cones that are not readily referred to modern groups of pine. Most of the Cretaceous cones whose internal structure has been examined represent *Pityostrobus*, an ancestral plexus from which *Pinus* had emerged by the Early Cretaceous (ca. 130–125 Ma) (Alvin, 1960). More numerous fossil pines come into the record in the Eocene, and they increased in abundance down to the present.

Pinus now includes 95 species that have been grouped into three subgenera, *Ducampopinus, Strobus,* and *Pinus* (Table 1). Of the 15 subsections, only three occur in both North America and Eurasia, notably *Cembrae* and *Strobi* of Subgenus *Strobus,* and *Sylvestres* of Subgenus *Pinus*. The 11 subsections in North America (Subgenus *Strobus* with four, Subgenus *Pinus* with seven) include about 62 taxa, or nearly two-thirds of all pine species. These are concentrated in Mexico with 28 species, and in California with 20. Larger regions elsewhere have fewer species, notably eastern Asia (14 spp.), southern Asia (seven spp.), and southern Europe (eight spp.).

To infer the modes and times of origin of these groups, and the manner in which present distributions may have developed, we turn to the fossil record. It is incomplete, yet it does contain the only historical facts (fossils) available for analysis. Interpretations of these remains may vary, because investigators have concentrated on different modes of analysis. Some have studied the internal structure of cones and needles where these have been available, though they are indeed few in number. Most remains of Tertiary pines occur as imprints in fine tuffaceous shale and sandstone preserved in lake beds and floodplain deposits of Cenozoic age. Both lines of evidence are reviewed here so as to arrive at a provisional, and hopefully better, understanding of pine history in North America.

EARLY ORIGIN AND EVOLUTION

Some fossil ovulate cones outwardly similar to those of *Pinus* have been designated *Pityostrobus*. They differ internally from *Pinus* cones in several ways (Miller, 1976). All of the presently known 20-odd Cretaceous cones that have



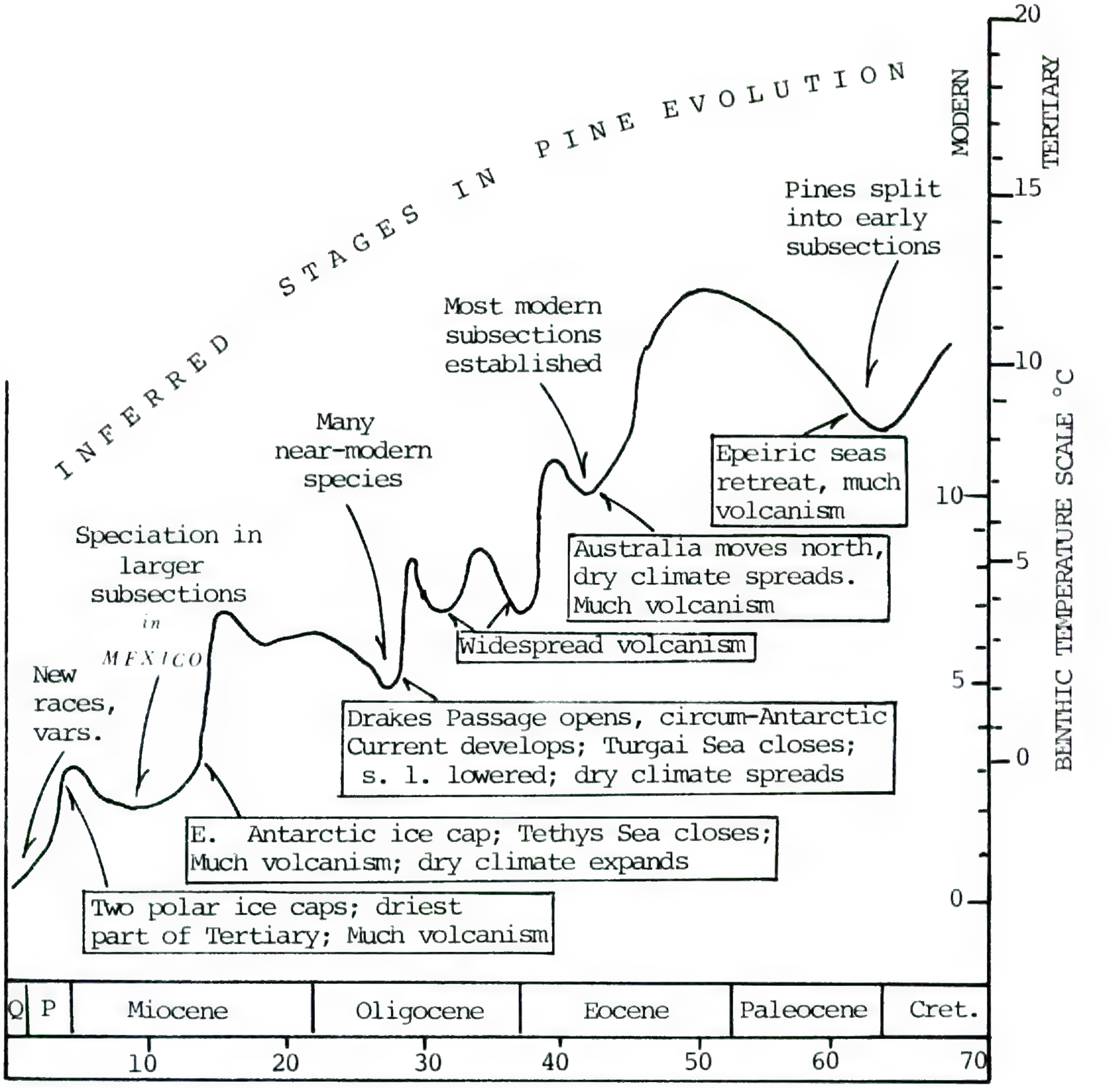
TEXT-FIGURE 1.—*A*. Diagrammatic sketch of some principal features of a *Pinus* cone scale.—*B*. Cone scale stripped of bast tissue.—*C*. When immersed in water and dried the cone scale flexes first toward the cone axis (*a*) and then away from it (*b*).—*D*. Cross section of half of a cone scale. The thick dorsal plate of sclerenchymatous cells (*a*) and a thinner ventral plate (*c*). Soft brown tissue (*b*) encloses vascular strands (*d*). Resin ducts (*e*).—*E*. Vascular strand enlarged. (Figs. B–E from G. R. Shaw, with permission of Arnold Arboretum.)

been examined structurally may have none or one or two of the internal features of *Pinus* (Miller, 1976, table 2). These include an inflated scale apex, bract-scale trace united at origin, resin canals abaxial to vascular tissue in the scale base, and scale strands curved on abaxial side (Text-Fig. 1). The first three features are present only in *Pinus* cones. The fourth is in all *Pinus* species and is rare and atypical in cones of other pinaceous genera (Miller, 1976, 1977a). The reviews by Miller (1976, 1977a) make it apparent that *Pityostrobus* is central to pine evolution. Inasmuch as *Pinus belgica* Alvin (1960) is in the Early Cretaceous (ca. 120–125 Ma), and represents Subgenus *Pinus* (Miller, 1977a) on the basis of its internal structure, it demonstrates the antiquity of the subgenus. In his reviews of Mesozoic conifers, Miller (1976, 1977a) noted that leaves with internal structure of two vascular strands also indicate affinity with Subgenus *Pinus*. Cretaceous cones reportedly allied to Subgenus *Strobus* may represent *Pityostrobus,* but these have not been examined internally. Certainly by the Eocene, species of the *Strobus* alliance were well established (see below).

Most described Cretaceous species of *Pityostrobus* and *Pinus* now occur at middle-high latitudes, as in Belgium, England, Massachusetts, Virginia, and New Jersey. However, the evidence of plate tectonics (Smith et al., 1981) shows that these areas were near Lat. 30–35°N in the Jurassic-Early Cretaceous. Climates were seasonally dry as shown by saline deposits and red beds (Hallum, 1984). By the Paleocene, pines were present at higher latitudes (70–80°N), although a cone of *Pityostrobus* (*P. lynnii* Berry) is recorded from the Paleocene of Virginia (Miller, 1977b). Available evidence suggests that the *Pityostrobus* plexus originated over low-middle latitudes and that it probably gave rise to *Pinus* by the Late Jurassic. *Pinus* was then adapted to seasonal climate in middle latitudes, as well as in the montane subtropics, and had spread into seasonal climates of middle and higher latitudes by the close of the Cretaceous (ca. 65 Ma).

Mirov (1967) inferred from both their morphology and physiology that modern pines originated not in uniformly hot, humid climates, but in those with alternating seasons, either wet and dry, or warm and cold, or a combination of both. Most living pines occur where there is ample sunshine, where the soil is porous, generally poor in nutrients, and well drained. They are xerophytes, for they withstand considerable drought and most show little tolerance of shade. Most pines inhabit exposed slopes away from rich, mesic valley forests. They now occupy diverse climates, ranging through temperate forested regions up to timberline, to semi-arid plateaus and desert-border environments, and to the tropics where there is a prolonged dry season, as in Cuba, Haiti, Nicaragua, Taiwan, Luzon, and Laos.

Their early adaptation to seasonal conditions no doubt favored their ability to seize new environmental opportunities later in their history. Diversity of terrain developed during the Laramide orogeny in the Late Cretaceous-Early Tertiary. This may well have been a time of splitting into forerunners of the principal subsections, the species of which are now extinct. By the Middle Eocene (ca. 45 Ma), there was a major shift to spreading dry climate in southwestern North America (Text-Fig. 2). This created conditions favorable for speciation in *Pinus*. In addition, active volcanism, extending from Wyoming-Montana southward through the Sierra Madre Occidental, Mexico, provided new, drier sites for the origination of taxa in spreading seasonal climate. By the Late Eocene (35 Ma), dry climate covered much of the western interior and far south into Mexico, and more seasonal conditions were developing (Axelrod & Raven, 1985). Continuing volcanism into the Oligocene (ca. 26.5 Ma) favored further diversification as indicated by the occurrence of numerous near-modern species. At this time, evolution was enhanced by the spread of drier conditions. As Drakes Passage opened, colder water that developed around Antarctica subsided and spread northward to rise in the low–middle latitudes, bringing drier climates there. In addition, as sea level was rapidly lowered in the Late Oligocene (ca. 27–26 Ma) (Vail et al., 1977; Vail & Hardenbol, 1979), more land area was exposed and continentality increased. With lowered base level, landscapes were rejuvenated by erosion, creating new slopes for occupation by pines and other plants adapted to drier, well-drained sites. Environments would be affected in both coastal and interior areas. In the coastal strip, the spread of drier sites may account for speciation of some *Australes* in the southeastern states. In the interior, new species of *Ponderosae, Oocarpae,* and *Cembroides* may have arisen, especially since tectonism and volcanism were active there. Middle Tertiary environments appear to have been similar to those now in the uplands of Mexico where active speciation is occurring today, and has in the recent



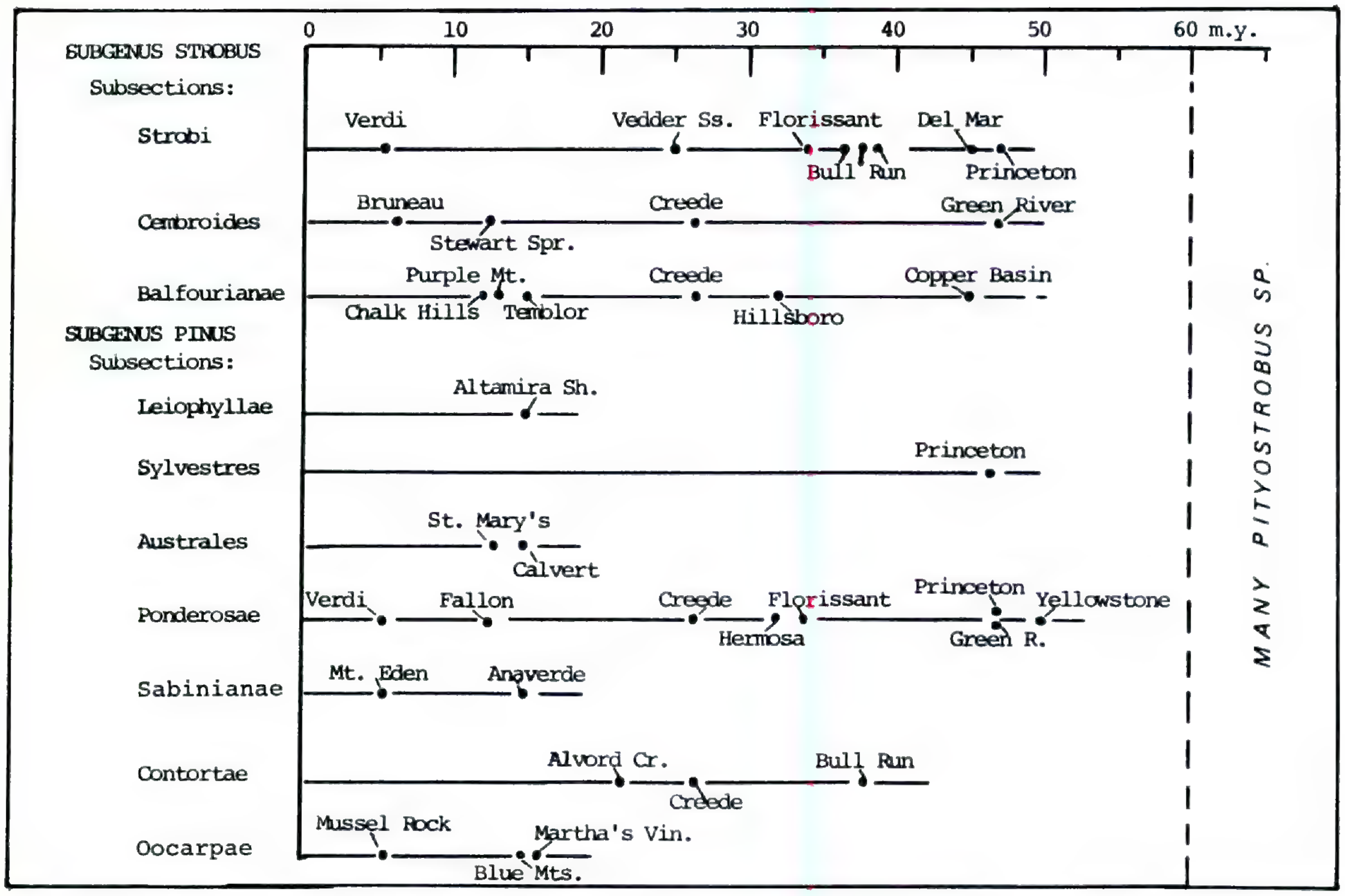
TEXT-FIGURE 2. Inferred correlation of environmental changes with pine evolution. Temperature curve from Savin, 1977. Early adaptation to drier, poorer sites aided by their association with ectotrophic mycorrhizae enabled pines to diversify as these conditions spread during the Tertiary.

past (Mirov, 1967: 341–345). Speciation was further enhanced in the late Cenozoic by fluctuating climate, the building of major volcanos, uplift of plateaus and bordering mountains, and the spread of drier and colder climates to which the taxa were adapted—all conditions favoring major, rapid changes in populations (Stebbins, 1974).

The ages of the older Tertiary species that may be assigned to American subsections of Subgenera *Strobus* and *Pinus* are indicated in Text-Figure 3. It is evident that their origins lie in earlier times, as the preceding inferences regarding environmental changes suggest. This may also be inferred from the distributions and ecological adaptations of taxa of *Pinus* subsections.

1. In Subgenus *Strobus,* the four species of Subsect. *Cembrae* have widely discontinuous distribution across Holarctica. *Pinus albicaulis* is in the high mountains of the western United States and adjacent Canada, *P. cembra* occupies the mountains of southern Europe, and *P. pumila* and *P. sibirica* range widely across central and eastern Siberia (Text-Fig. 4).

2. In Subgenus *Strobus* (Text-Fig. 5), Subsect.



TEXT-FIGURE 3. Ages of fossil pines of American subsections of Genus *Pinus*.

Strobi has 14 species widely scattered in forests across middle to low-middle latitudes in North America from southern Canada to El Salvador and Guatemala, and in Eurasia from Japan to the Himalayas and Vietnam, and to Albania in southern Europe.

3. In Sect. *Parrya* (Text-Fig. 6), Subsect. *Cembroides* (8 spp.) occupies the drier parts of western North America, whereas Subsect. *Balfourianae* (3 spp.) is in moister and/or colder montane regions. Taxa of these two subsections are very different morphologically and ecologically and also differ greatly from species of Subsect. *Gerardianae* (2 spp.) now in the Pamir region (*P. gerardiana*) and north-central China (*P. bungeana*).

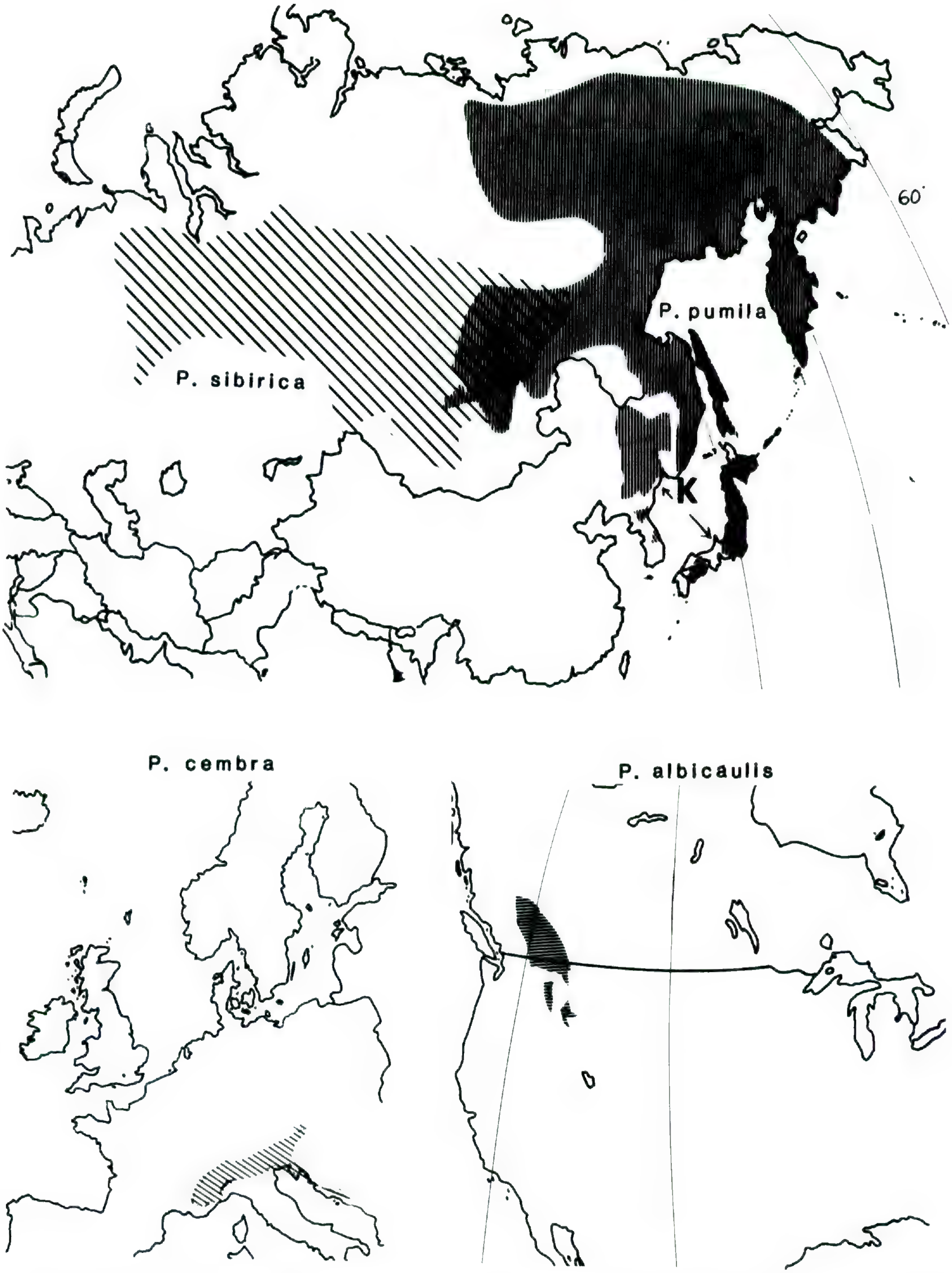
4. Sect. *Ternatae* includes Subsect. *Leiophyllae* (2 spp.) in Mexico and southern Arizona, Subsect. *Canarienses* (2 spp.) of the Canary Islands (*P. canariensis*) and the Himalayas (*P. roxburghii*), and Subsect. *Pineae* (1 sp.) of southern Europe-Asia Minor (*P. pinea*) (Text-Fig. 7).

5. In Sect. *Pinus*, Subsect. *Sylvestres* with 19 taxa is chiefly Eurasian. The two American species are adapted to dissimilar climates, cold temperate for *P. resinosa*, tropical for *P. tropicalis*. A similar disjunction in adaptation is apparent for the 17 Eurasian taxa (Text-Fig. 8), the temperate species of which are presumably derived.

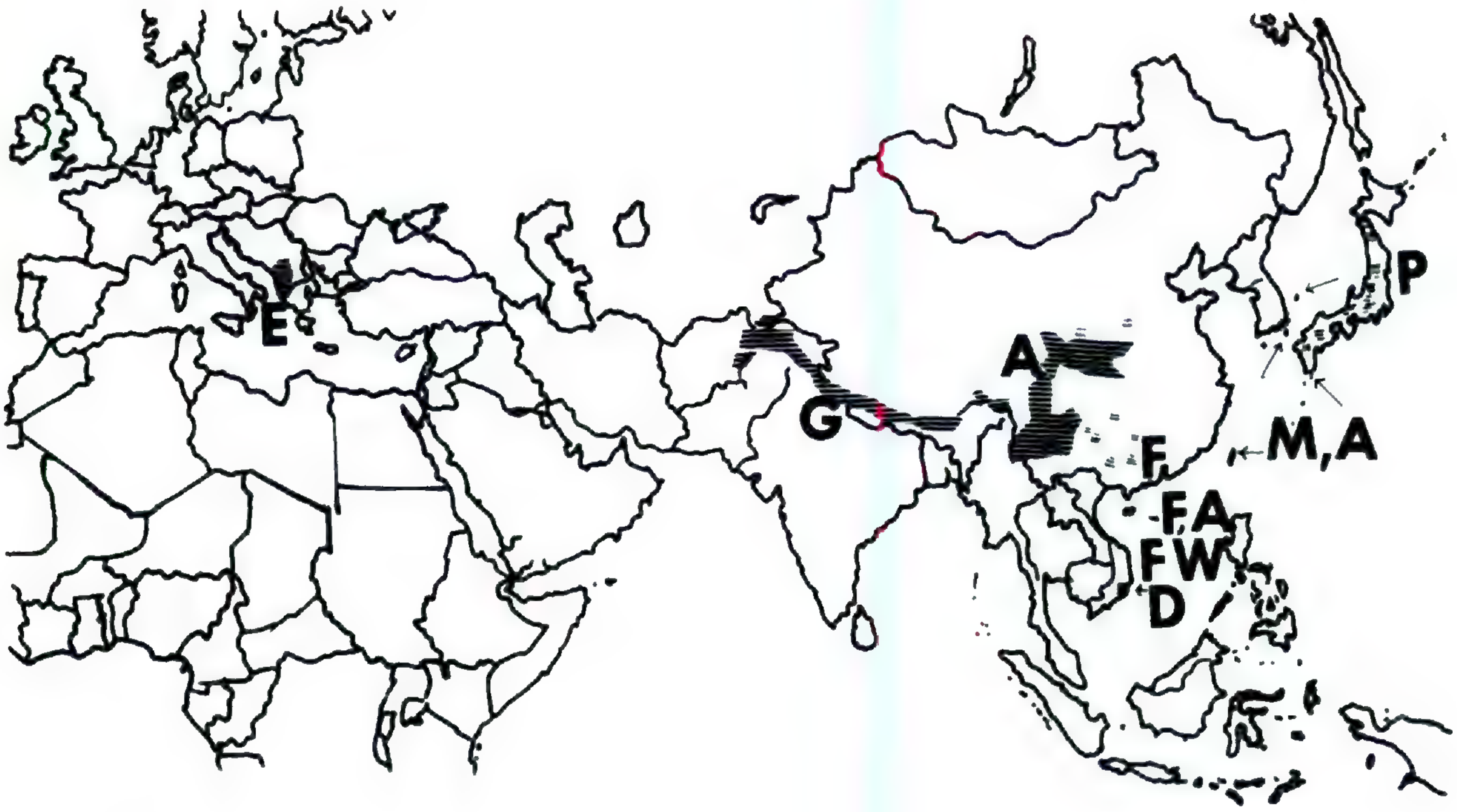
The distinctness of these subsections (see Little & Critchfield, 1969), their disparate distributions (see Critchfield & Little, 1966), and their different climatic adaptations, all imply considerable age. This inference is supported by the fossil record, for most of these alliances occur in the Oligocene, and some are represented by taxa in the Eocene (Text-Fig. 3). The evidence again suggests that evolution of the modern subsections was well under way in the Eocene and probably had commenced earlier for some, relations consistent with comparative immunological and amino acid sequence studies of proteins (Prager et al., 1976).

TERTIARY HISTORY OF AMERICAN SUBSECTIONS

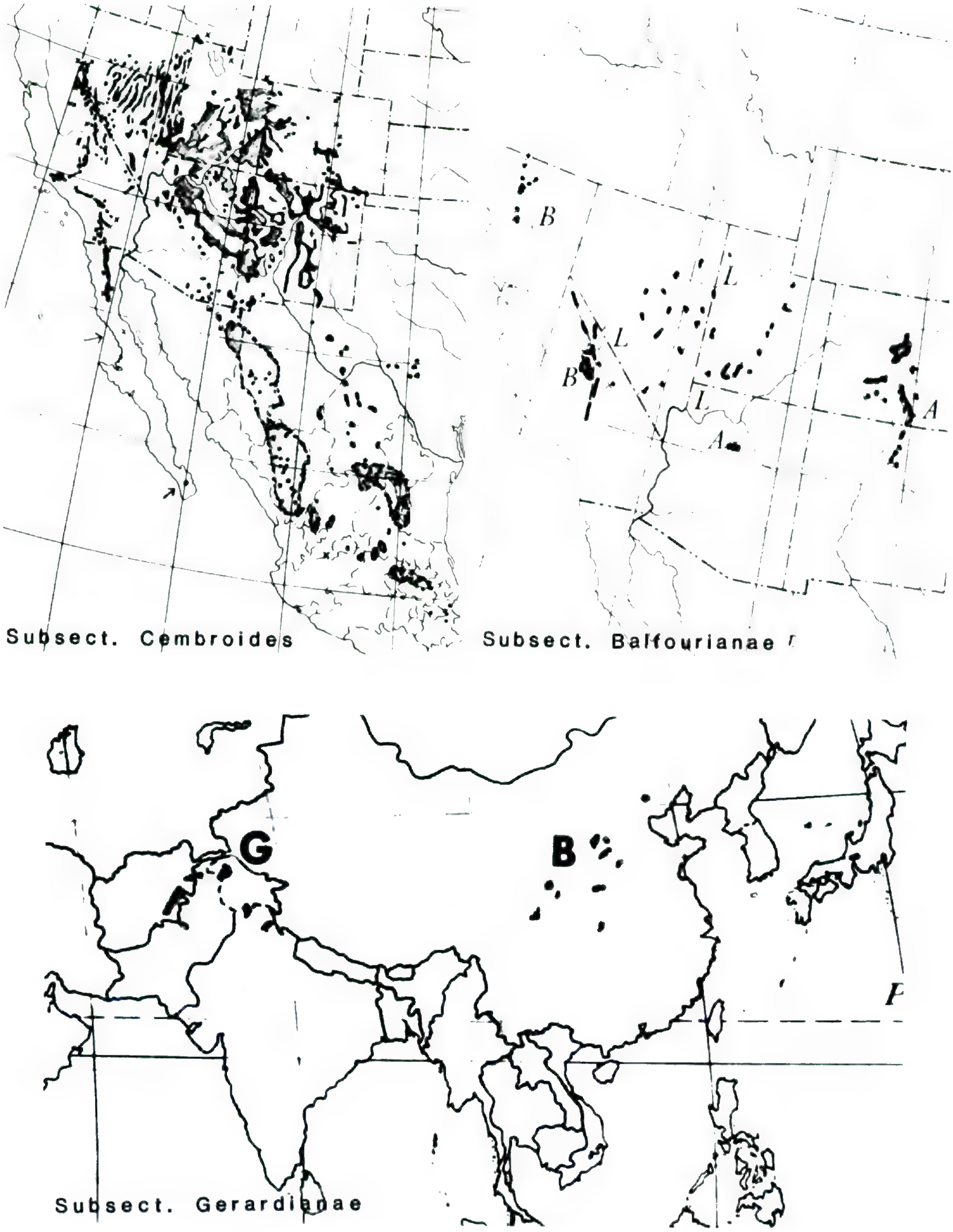
The records of Tertiary pines indicate that species of three subsections (e.g., *Cembrae, Sylvestres, Strobi*) now common to North America and Eurasia probably were established by the Paleogene. By contrast, eight subsections now restricted to North America, and the four to Eur-



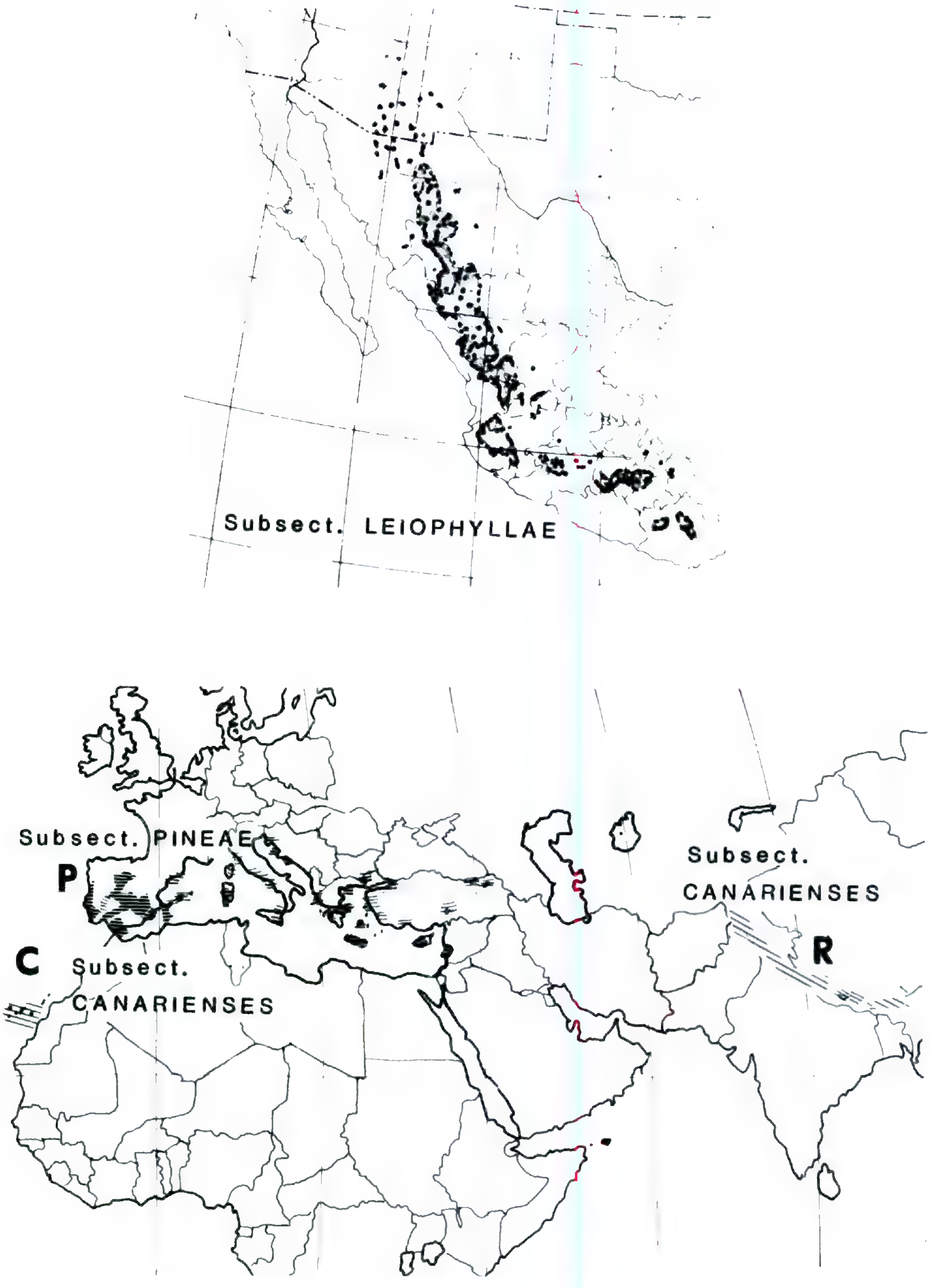
TEXT-FIGURE 4. In Sect. *Strobus*, Subsect. *Cembrae* has a discontinuous distribution across Holarctica (K = *P. koraiensis*). The Eurasian taxa have finely serulate needles, the American is entire. Was *Cembrae* represented in northeastern North America during the later Tertiary?



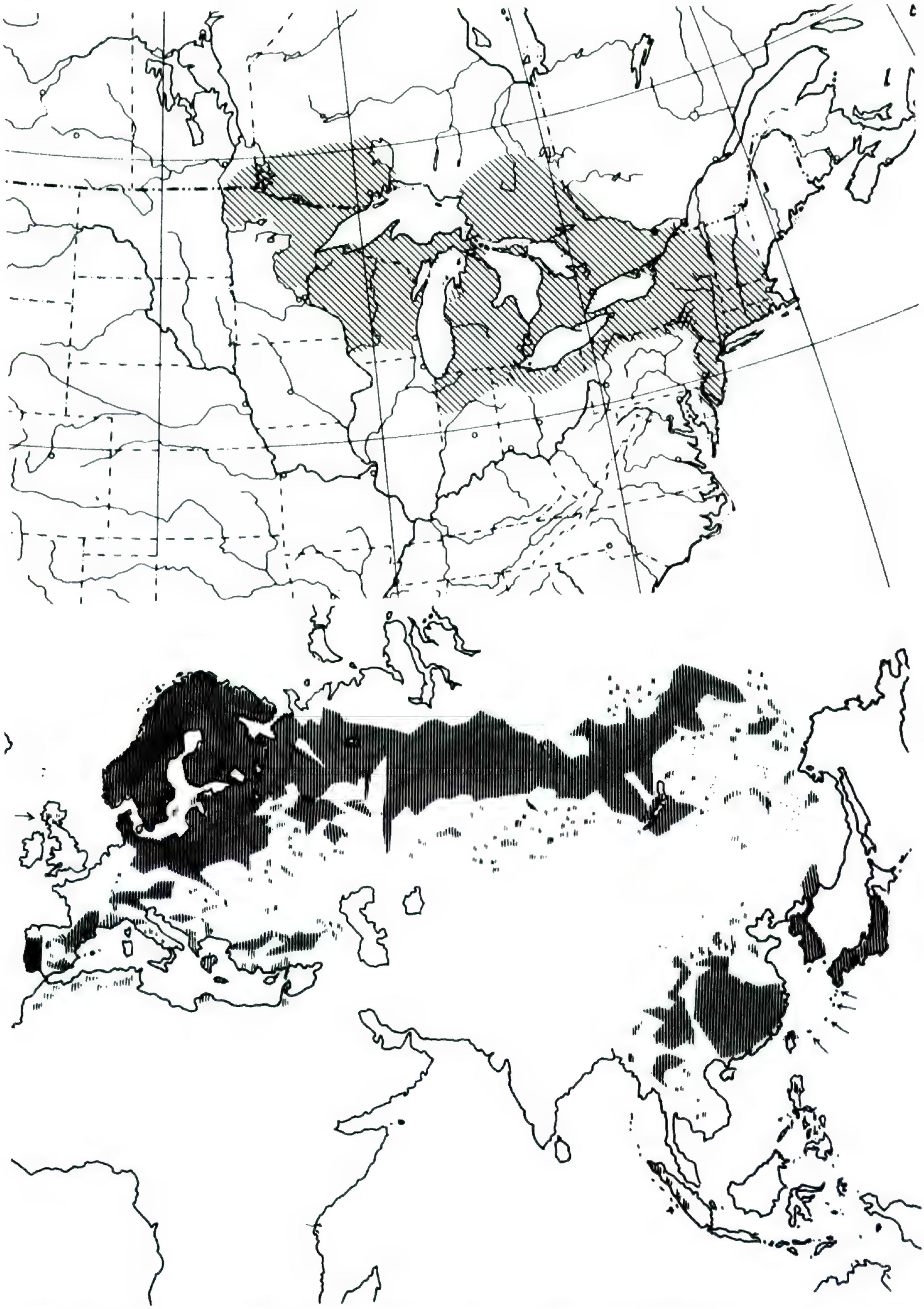
TEXT-FIGURE 5. In Sect. *Strobus*, Subsect. *Strobi* has eight species in Eurasia (E—*P. peuce*, G—*P. griffithii*, A—*P. armandii*, P—*P. parviflora*, F—*P. fenzeliana*, D—*P. dalatensis*, M—*P. morrisonicola*, and W—*P. wangii*), whereas there are six species in North America (S—*P. strobus*, M—*P. monticola*, F—*P. flexilis*, L—*P. lambertiana*, St—*P. strobiformis*, A—*P. ayacahuite*). Note that *P. strobus* is also in southern Mexico (Chiapas) and Guatemala.



TEXT-FIGURE 6. In Sect. *Parrya*, Subsect. *Cembroides* has eight species in southwestern North America (*P. edulis, P. cembroides, P. monophylla, P. quadrifolia* in the United States; *P. culminicola, P. maximartinezii, P. pinceana, P. nelsonii* in Mexico). Subsect. Gerardiana has two species (G—*P. gerardiana* in the Pamir region, B—*bungeana* in central China), and Subsect. *Balfourianae* has three species (B—*P. balfouriana*, L—*P. longaeva*, A—*P. aristata*) in the western United States.



TEXT-FIGURE 7. In Sect. *Ternatae,* Subsect. *Leiophyllae* with two species (*P. leiophylla, P. lumholtzii*) ranges from southern Arizona-adjacent New Mexico to southern Mexico. Subsect. *Pineae* (one species, P—*P. pinea*) is on the north shore of the Mediterranean Sea. Subsect. *Canarienses* has two species (C—*P. canariensis,* R—*P. roxburghii*) discontinuous from the Canary Islands to the Himalayas. Such disjunctions clearly attest to a long history.



TEXT-FIGURE 8. In Sect. *Pinus*, Subsect. *Sylvestres* with 19 species is largely Eurasian. Only two species are in North America: *P. resinosa* in northeastern USA-adjacent Canada and *P. tropicalis* in Cuba. The alliance has adapted to climates ranging from tropical (Cuba, Vietnam, Sumatra, Phillipines) to Mediterranean, to cold

TEXT-FIGURE 9. Similar cones are produced by *P. albicaulis* and *P. sibirica*. The species differ in that *P. albicaulis* needles are entire, while those of *P. sibirica* are finely serrulate; and *P. sibirica* is a tall tree, *P. albicaulis* is bushy.

asia, appear to be autochthonous as judged from present fossil evidence.

SUBSECT. CEMBRAE

Of the five species in this group, *P. cembra, P. koraiensis, P. pumila,* and *P. sibirica* are in Eurasia, whereas *P. albicaulis* is chiefly at subalpine levels in northwestern North America. Cones of *P. albicaulis* are scarcely separable from those of *P. sibirica* (Text-Fig. 9). The chief differences between these taxa are in the needles (serrulate or not; stomatal position), characters that may have developed following the spread of ancestral taxa into the separate land areas. The age of the ties between these taxa is not known, although Tertiary cones from Eurasia have been compared with *P. cembra* (Gaussen, 1960: 228) and other species (e.g., *P. koraiensis*) reportedly have allied taxa in the Paleogene (Gaussen, 1960). Since fossil records indicate that a *cembra-sibirica*-like pine was present in the Paleogene of Eurasia, an ancestral species allied to them, and to *P. albicaulis,* probably ranged earlier across boreal regions to give rise to separate species in each area, with *cembra-sibirica-pumila* representing chiefly

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temperate in northern Europe and Asia where it reaches above Lat. 60°. Its occurrence in diverse climates in America implies different times of entry, probably Early Paleogene-Late Cretaceous for the ancestor of *P. tropicalis,* as compared with Miocene for *P. resinosa* in northeastern U.S. and Canada.

TEXT-FIGURE 10. Cones of *P. griffithii* from the Himalayas are quite similar to those of *P. monticola* of western North America.

varietal differences across Eurasia. Whereas *P. albicaulis* is a small bushy tree in most of its area, the Eurasian *cembra-sibirica* commonly form tall forest trees. *Cembrae* have a wide occurrence in eastern and central Asia as compared with their restricted areas in the Alps and western North America (see maps in Critchfield & Little, 1966). Since the latter areas were largely under ice sheets during the Quaternary, glaciation may account for these present restrictions as well as the absence of *Cembrae* from eastern North America.

SUBSECT. STROBI

Modern species of this alliance are now Holarctic in occurrence. In North America are *P. strobus* (northeastern U.S.-Canada), *P. strobus*

var. *chiapensis* (southern Mexico-Guatemala), *P. monticola* (California-Washington-Idaho-British Columbia), *P. lambertiana* (Baja California Norte, California, Oregon), *P. flexilis* (Alberta-New Mexico-eastern California), *P. strobiformis* (southern Rocky Mountains-northern Mexico), *P. ayacahuite* (southern Mexico-Guatemala). The Eurasian taxa are widely scattered as shown by *P. peuce* (Balkans), *P. armandii* (central China), *P. griffithii* (Himalayas), *P. parviflora* (Japan), *P. morrisonicola* (Taiwan), *P. fenzeliana* (Hainan), *P. wangii* (S. Yunnan), and *P. dalatensis* (Vietnam). Since fossil cones of the general sort produced by these pines are in the Late Cretaceous (some may be *Pityostrobus*), the intercontinental links are old. The occurrence of numerous, presently Asian taxa in North America in Paleocene to Miocene floras (e.g., *Ailanthus, Cercidiphyllum, Ginkgo, Glyptostrobus, Cunninghamia, Metasequoia, Phoebe*) suggests that in favorable montane areas, ancestral *Strobi* populations probably extended across both the Beringian and mid- to North Atlantic regions, thence diverging into allied species as they spread southward on each landmass.

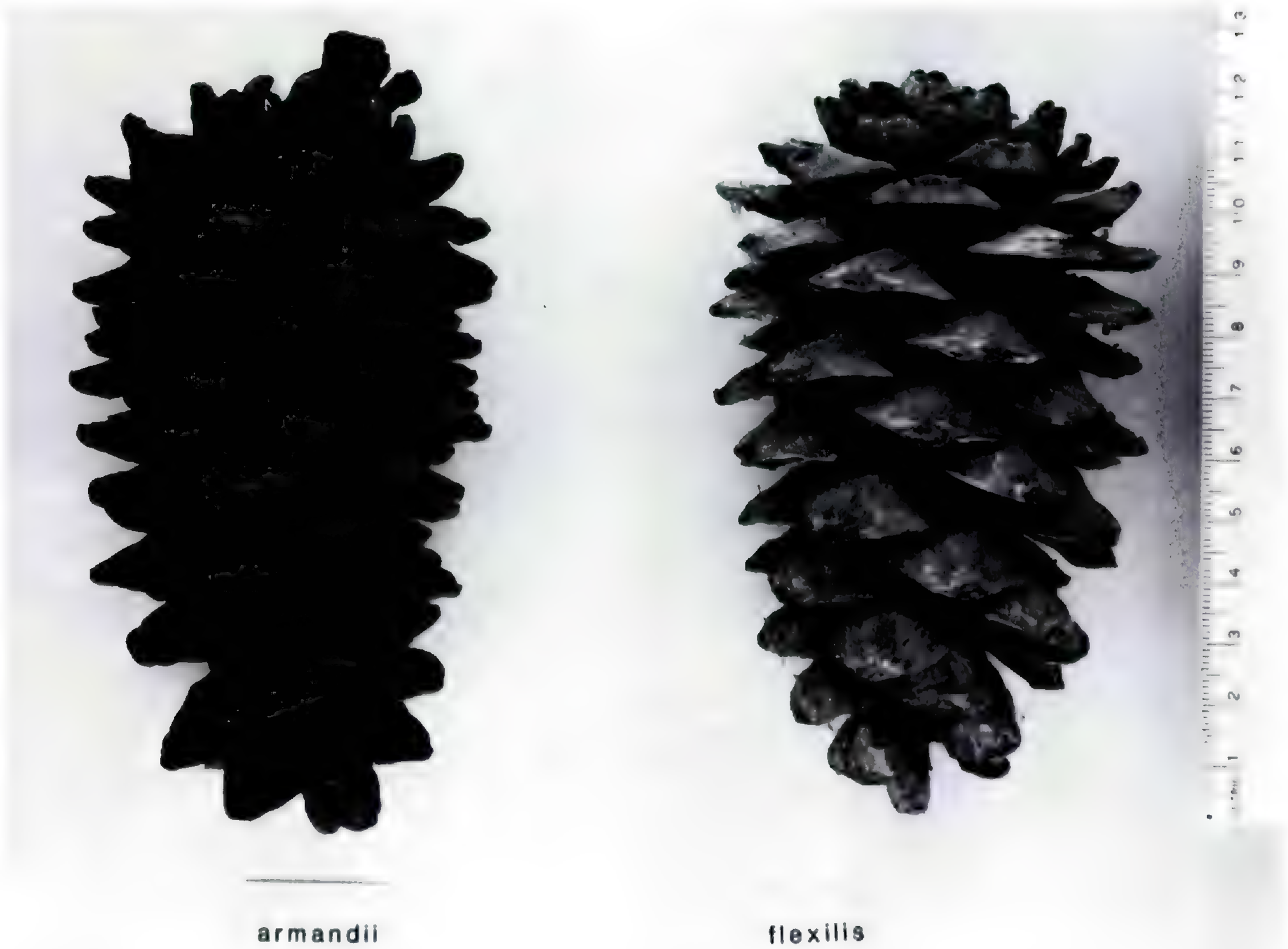
The white pines, *P. strobus* and *P. monticola*, of eastern and western North America are paired-species, and these are allied also to the Himalayan *P. griffithii* (Text-Fig. 10). Both alliances may represent species of an ancestral population that spread south into each landmass and then diverged into related species east and west. This inference is supported by the internal structure of needles of *P. similkameenensis* (Miller, 1973; Stockey, 1984), preserved in cherts of Middle Eocene age near Princeton, British Columbia. This 5-needled pine is referable to Sect. *Strobus*, showing that the alliance was already in the Rocky Mountains 47 Ma ago. This implies that an early Paleogene (or older) link between allied intercontinental species may be inferred because needles of different *Strobi* species are indistinguishable in X-sectional anatomy (Harlow, 1931).

Reports that the American *P. monticola* has a fossil record in Siberia (Mirov, 1967; Wolfe & Leopold, 1967) are unsubstantiated. The cone of *P. monticola fossilis* (Sukachev, 1910) from the Pliocene is more robust and has larger, thicker cone scales, and is not so slender as *P. monticola* cones that are closed (from immersion in water) like the Siberian fossils. A similar, more complete cone is *P. itelmenorum* Vassek. from the Mammoth Mountain flora of Middle Miocene age on the Aldan River (Dorofeev, 1969). Both fossil species are more nearly allied to *P. armandii* from the uplands of central China.

Pinus flexilis from the western interior seems allied to *P. armandii* of central China, which also inhabits cooler montane areas (Text-Fig. 11). An ancestral population may have spread south in the interior, giving rise to paired taxa that diverged chiefly in needle structure (entire or serrate; position of stomata) and seed wings (absent in *P. armandii*, attached to cone scale in *P. flexilis*) in each region. This would have been early, for *P. florissanti* Lesquereux (cf. *P. flexilis*) is in the Florissant flora, Colorado (MacGinitie, 1953), dated at 34 Ma (Epis & Chapin, 1975).

The preceding links between North American and Eurasian white pines follow Shaw's (1914, 1924) reclassification of his *Cembra* Groups (*Cembrae, Flexiles* and *Strobi*) into *Cembrae* and *Strobi*. Species of these morphologic alliances differ in chemical composition of their turpentines (Mirov, 1953, fig. 1). This is expectable for, as suggested for the differences in needle structure, the chemical differences may also have developed as the early populations spread into each landmass.

The Cordilleran white pines, *P. flexilis-strobiformis-ayacahuite*, that stretch from the Canadian Rockies into Guatemala, seem to form a natural series. The question arises as to whether the Eocene (ca. 48–47 Ma) *P. delmarensis* Axelrod from near San Diego, which was then opposite Guaymas, Mexico (Gastil & Jensky, 1973), may be a part of this alliance. Its present position results from displacement northward as the San Andreas rift system was activated, separating *P. delmarensis* from any Mexican connection (Text-Fig. 12). Although *P. delmarensis* seems closely allied to *P. lambertiana* of California, genetic studies indicate that *lambertiana* crosses with Asian pines (*P. armandii, P. koraiensis*), not with American taxa (Mirov, 1967: 334). Since crossing experiments with the Mexican taxa are incomplete (W. B. Critchfield, pers. comm., May 1984), the data are insufficient now to resolve the problem. Structurally, *P. delmarensis* seems closely allied to *P. lambertiana* and may represent an early, western segregate of a group that gave rise to *P. strobiformis-ayacahuite* in the interior. The suggested affinity is supported by the occasional occurrence of moderately reflexed cone scales in *P. lambertiana*, a feature typical of *P. strobiformis* and *P. ayacahuite* cones (Text-Fig. 13). Furthermore, all these taxa have broadly ovate seed wings with rounded tips, not



TEXT-FIGURE 11. Judging from their similar cones, *P. armandii* and *P. flexilis* appear to be paired species. They differ in that *P. armandii* has finely serrulate needles, whereas those of *P. flexilis* are entire. *Pinus armandi* seeds are wingless, and those of *P. flexilis* have the seed wings attached to the scales.

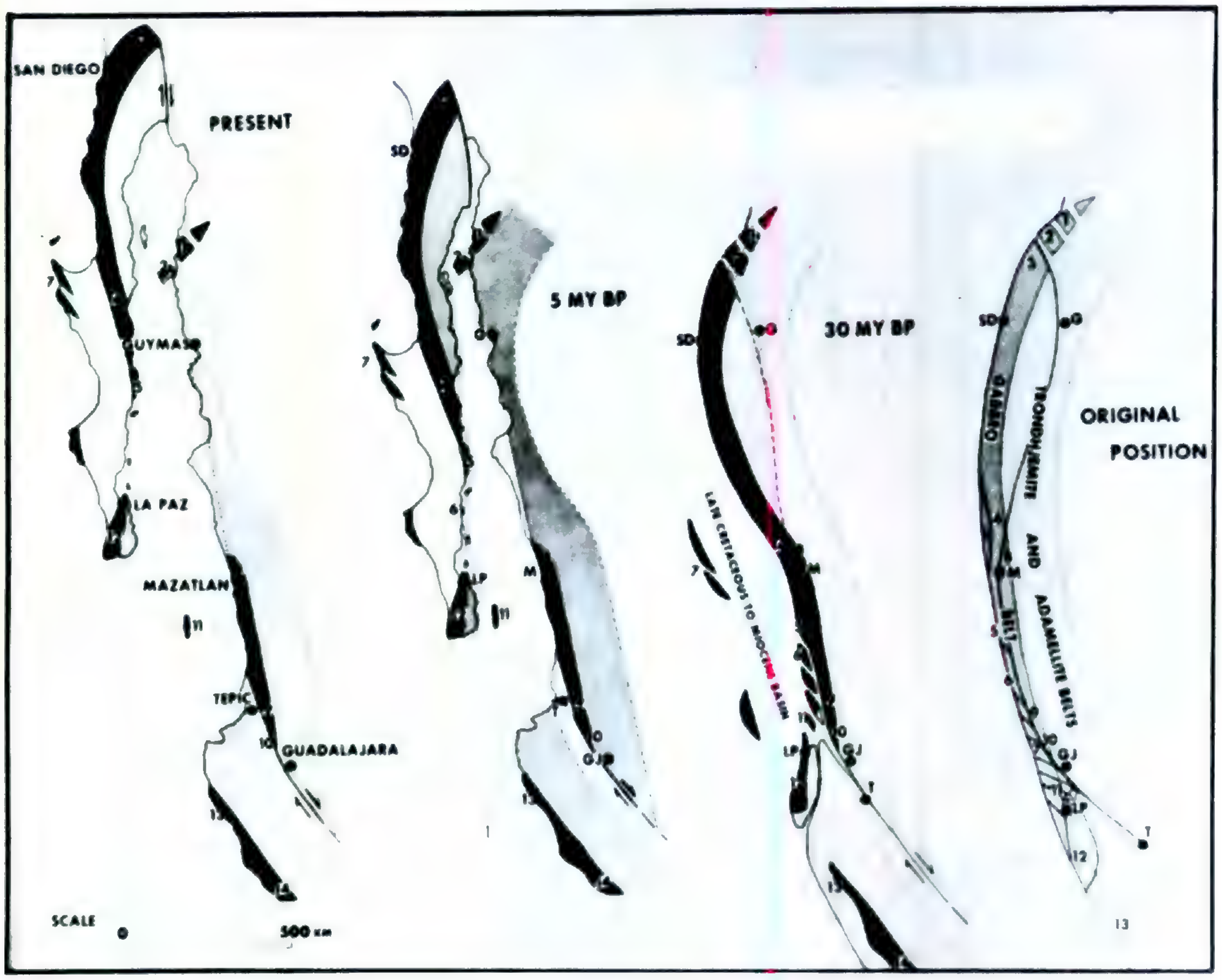
slender wings with acute tips as in *P. monticola* and *P. strobus*.

SUBSECT. CEMBROIDES

Records of this alliance occur in the mid-Eocene Green River flora (47 Ma) of northern Colorado-adjacent Utah (MacGinitie, 1969), and in the Late Oligocene Creede flora (26.5 Ma), southwestern Colorado (Axelrod, unpubl. data). Younger records are in the mid-Miocene Tehachapi flora (17 Ma) of the western Mohave region (Axelrod, 1939), the Stewart Spring flora (13 Ma) of southwestern Nevada (H. Schorn, pers. comm.), and in the Chalk Hills Formation (5–6 Ma) near Bruneau, Idaho (Knowlton, 1901; Brown, 1940; Malde & Powers, 1962). That *Cembroides* do not hybridize with other pines (Mirov, 1967: 569) and have been in existence since the Eocene, demonstrates that it is a very distinct subsection. This is suggested also by the observation that the woods of nut-pines have piciform lateral ray pits and thick-walled ray cells that approach in structure those of Cretaceous "pines" (Bailey, 1910).

The fossil piñons were chiefly subordinate members of rich woodland vegetation, whereas they now often dominate woodlands. The Idaho occurrence of *Pinus lindgrenii* Knowlton near Bruneau may be an exception. A number of cones have been recovered by local collectors, and a dozen or so are in the Jurupa Museum, Riverside. Their relative abundance suggests that Piñon may have had at least a subordinate role in the flora. This is consistent with their worn, eroded nature, which indicates transport, presumably from a piñon zone that covered warmer, south-facing slopes bordering the floodplain.

With respect to *Pinus cembroides* var. *cembroides*, the question may be raised as to whether *P. cembroides* var. *lagunae* Robert-Passini (1981) may not be the most ancient living member of the species. As described further by Bailey (1983), it differs from *P. cembroides* var. *cembroides* in



TEXT-FIGURE 12. Disruption of western Mexico and its northward displacement following 25 Ma ago (from Gastil & Jensky, 1973). Members of several *Pinus* subsections were displaced northward into the developing Mediterranean climate of California and border area.

its average longer needles, thinner fascicles, fewer stomatal lines, longer cone peduncles, and more obvious prickles on the umbos. In addition, I have noted that the trees are more robust and larger than *P. cembroides* var. *cembroides,* and the cones are larger than those of most populations in the Southwest and northern Mexico.

The var. *lagunae* inhabits uplands of the Cape Region, Baja California. The limited (10 year) record at La Laguna indicates a mean annual temperature of 14.5°C and an annual range of 7.5°C (Garcia, 1973). This gives the area a very equable climate—*M* 65 in Bailey's (1960, 1964) classification. The pine is a component of the piñon-madrone evergreen-oak woodland at altitudes generally from 1,600 to 2,000 m. The notion of its antiquity is consistent with the occurrence of other marked endemics or disjunct taxa in the area, notably *Garrya salicifolia, Populus brandegeei, Quercus albocincta, Q. devia, Q. rugosa, Q. tuberculata, Rhus tepetate,* a feature shown by upland floras of other insular regions (Cedros Island, Canary Islands, Revillagigedo Islands, Madeira Islands, Juan Fernandez Islands, and others). The Cape Region was isolated from the mainland following 25 Ma ago (Text-Fig. 12), and the Gulf opened about 5–6 Ma ago, as judged from sea-floor spreading anomalies (Gastil & Jensky, 1973). Persistence of relict taxa in the uplands there thus seems understandable from both a geologic and climatic standpoint. The differences between *P. cembroides* var. *lagunae* and other taxa of the *cembroides* complex (see Bailey, 1983; Bailey & Hawksworth, 1979, 1983; Bailey & Wendt, 1979; Little 1966, 1968; Robert-Passini, 1981), involve their shorter needles, thicker fascicles, and other features that presumably reflect more recent adaptation to increasing aridity in areas bordering the Mexican plateau.

SUBSECT. BALFOURIANAE

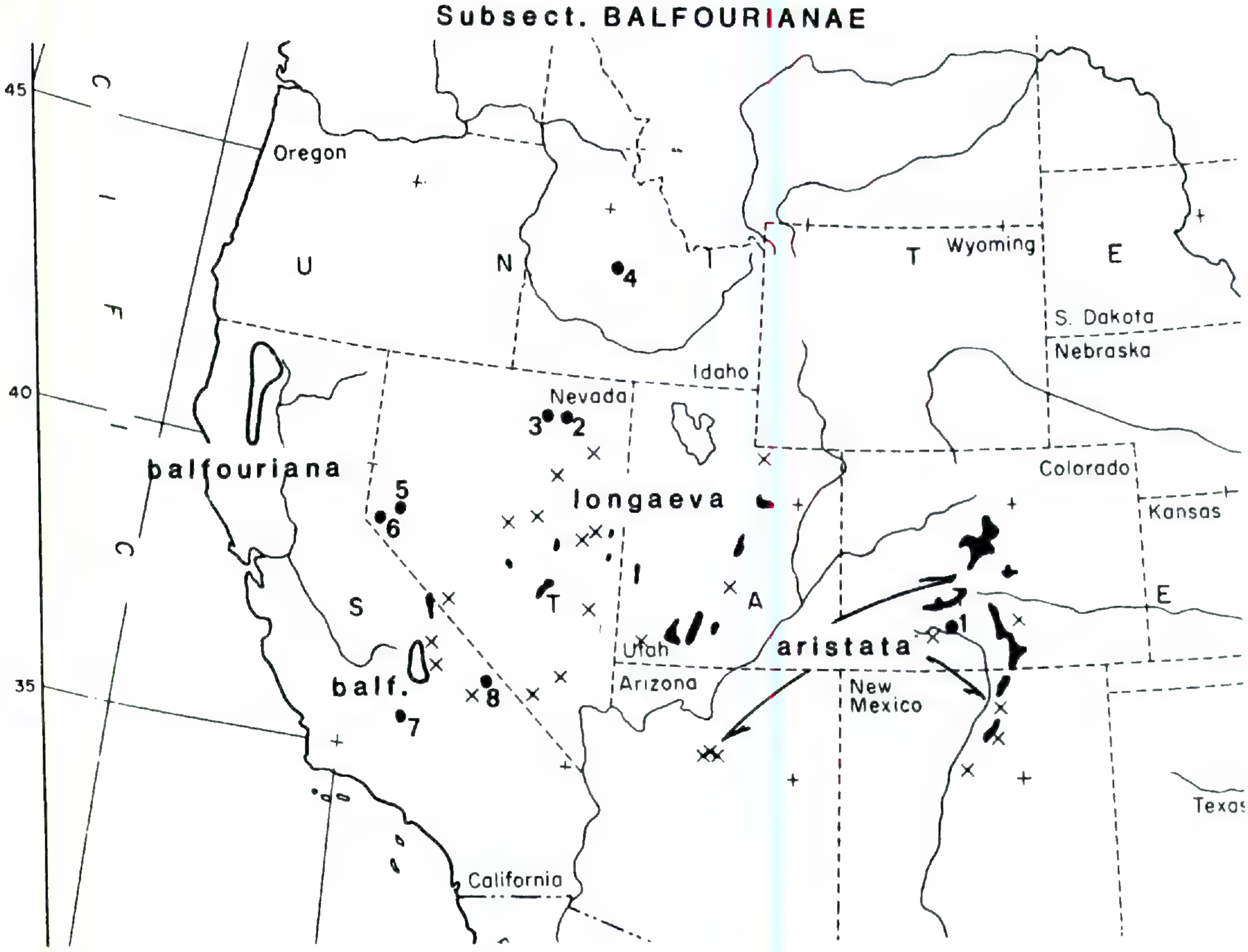
This small alliance includes three taxa, *P. aristata* Engelm. of Colorado-northern New Mexico and northern Arizona, *P. longaeva* Bailey of Utah and the Great Basin, and *P. balfouriana*

TEXT-FIGURE 13. *Pinus lambertiana* is allied to *P. delmarensis* from Middle Eocene rocks near San Diego. The Californian taxa were isolated from the related Mexican *P. strobiformis-ayacahuite* by movement on the San Adreas rift system.

Murray, which is disjunct in California from the Klamath Mountain region to the southern Sierra Nevada, 625 km (390 mi.) distant. Their detailed distribution is charted by Bailey (1970, fig. 3).

There are fossil records of two of these taxa (Text-Fig. 14). *Pinus aristata* is scarcely separable from *P. crossii* Knowlton from the Creede flora (26.5 Ma), Colorado, where the branches of *P. aristata* overhang some of the fossil sites today. *Pinus crossii,* abundantly represented at Creede by cones, foliage, and winged seeds, lived adjacent to a rich piñon-juniper woodland, a community usually well removed from *P. aristata* today. Cones and foliage of *P. crossii* are also in the Hillsboro flora, central New Mexico, dated at 32 Ma. Its associates included spruce and several rare, small leaflets of *Mahonia.* This appears to have been a high montane site with a rich, or nearly pure, stand of fossil bristlecone pine (Axelrod & Bailey, 1976). A species allied to *Pinus crossii* was already in existence in the Late Eocene (40 Ma), as judged from winged seeds and a fascicle in the Copper Basin flora (Axelrod, 1966a), which represents a rich conifer-hardwood forest. This species also contributed to pure montane conifer forests in the Late Eocene Bull Run flora north of Elko, Nevada.

The distal half of a cone in the Lower Oligo-

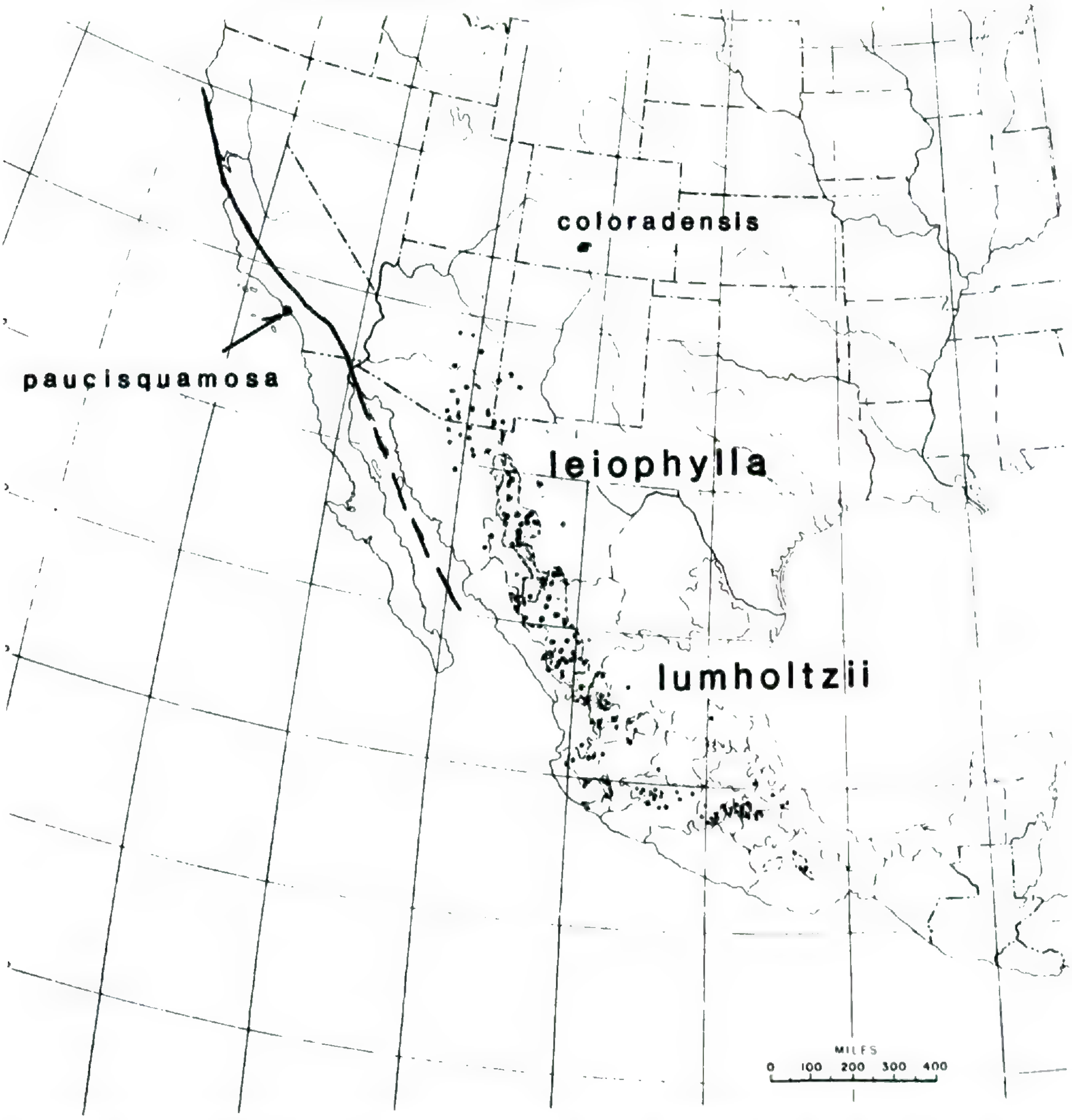


TEXT-FIGURE 14. Distribution of the three species of Subsect. *Balfourianae* (map from Critchfield & Little, 1966): *P. aristata, P. longaeva,* and *P. balfouriana.* Fossils of *P. crossii* Knowlton, allied to *P. aristata,* occur at 1—Creede, 2—Copper Basin, 3—Bull Run. *Pinus balfouroides* Axelrod, allied to *P. balfouriana,* is recorded at 4—Thunder Mt., 5—Purple Mt., 6—Chalk Hills, 7—Sharktooth Hill, and 8—Death Valley. Fossils related to *P. longaeva* are not now known.

cene (Chadronian) Titus Canyon Formation (Stock & Bode, 1935), Death Valley, appears to be *P. crossii.* Its affinity is suggested by the thin cone scales surmounted by low, near-terminal umbos, and by the generally ovate shape of the partially open cone. Its Early Oligocene occurrence in the southern Great Basin, as well as in northeastern Nevada in the Late Eocene, suggests that *P. crossii* probably originated in the western interior.

Pinus balfouroides Axelrod from the Oligocene Thunder Mountain flora, Idaho (in Brown, 1937), is represented by relatively large cones (+9 cm), as well as needles in 5s. Another Idaho record is in the Coal Creek flora (27 Ma), Lost River Range, where it is also associated with a humid conifer forest, including species of *Abies, Picea, Larix, Pinus, Tsuga, Chamecyparis,* and *Sequoiadendron. Pinus balfouroides* occurs in western Nevada in the Chalk Hills (Axelrod, 1962) and Purple Mountain (Axelrod, 1976b) floras. Dated at 12 and 13 Ma, respectively, the fossils include relatively small cones (6–7 cm long), as well as winged seeds and foliage. A cone is also in the marine Temblor Formation (15 Ma) at Sharkstooth Hill near Bakersfield, where it was transported from the Sierra Nevada into the marine basin.

The few fossil cones available suggest that in size the Thunder Mountain population is more nearly like that now in the Klamath Mountains where *P. balfouriana* var. *balfouriana* occurs, whereas the smaller cones in the western Nevada floras are comparable to the southern Sierran population, *P. balfouroides* var. *austrina* (Mastroguiseppe & Mastroguiseppe, 1980). The larger-coned, northern population, which has been in a more mesic climate since the Oligocene, shifted coastward during the Neogene to the humid Klamath Mountain area. By contrast, the smaller-coned *austrina* may have originated in the subhumid western Nevada region and moved



TEXT-FIGURE 15. Occurrence of species of Subsect. *Leiophyllae* in the past and today (map from Critchfield & Little, 1966). The coastal southern California occurrence of *P. paucisquamosa* Templeton in the Middle Miocene probably reflects displacement northward from Mexico (see Text-Fig. 12). The record of *P. coloradensis* Knowlton at Creede reflects the wider distribution of Leiophyllae in the Late Paleogene, a time when other fossil taxa with relatives now far to the south also ranged widely to the north.

into the southern Sierra Nevada as climate became drier. It survived there largely south of the Pleistocene ice cap. Since the close of the Wisconsin, it has spread some 40 km (25 mi.) north to its present northern area near Onion Valley, above Independence, an area under ice during Wisconsin glaciation.

SUBSECT. LEIOPHYLLAE

Fossil cones of *Pinus coloradensis* Knowlton, and foliage presumed to represent the species, occur in the late Oligocene Creede flora, Colorado. The fossils appear to represent the Leiophyllae, and show relationship to *P. chihuahuana* Engelm., also considered a variety of *P. leiophylla*. The fossil needles in 5s are shorter than those of the modern species. *Pinus leiophylla* ranges today from southeastern Arizona-adjacent New Mexico into southern Mexico (Oaxaca).

The well-preserved cone on *Pinus paucisquamosa* Templeton (1953) that represents this alliance comes from the marine Altamira Shale near Pt. Fermin, at the south end of Palos Verdes Peninsula, southern California (Text-Fig. 15).

Dated at 14.5 Ma, and of early Mohnian age, it was compared initially with *P. chihuahuana*. As judged from the broad cone scales of the fossil, it appears more nearly allied to the only other member of this alliance, *P. lumholtzii* of the Sierra Madre Occidental.

As with several other taxa, this record may have been transported to its present area by movement along the San Andreas rift system. This would place it at the latitude of northern Sonora in the Middle Miocene, an area close to members of the Leiophyllae today and an area where they probably were also in the past (see Text-Figs. 12, 15).

SUBSECT. SYLVESTRES

This alliance is represented in the Eocene of British Columbia as judged from the internal structure of cones and foliage preserved in the Allenby Formation (46 Ma) near Princeton (Stockey, 1984). The evidence indicates that cones of *P. princetonensis* Stockey, as well as the cone of *P. arnoldii* Miller and needles of *P. allisonii* Stockey have the characteristics of Subsect. *Sylvestres*. This suggests a Beringian connection with Eurasian members of the alliance in the Early Eocene or Paleocene.

The cones of *P. clementsii* Chaney (1954) from the Late Cretaceous (85–86 Ma) of southern Minnesota were compared by Mirov (in Chaney) with the living *P. resinosa* Aiton. However, the preservation of the mold that represents the holotype (Chaney, 1954, figs. 1, 2) is poor, and the features of the umbo are not clear. The paratype (Fig. 6) is an incomplete specimen, and neither specimen has internal structure preserved. These specimens, from localities 40 km (25 mi.) apart, appear to be different species. They may represent the genus *Pityostrobus*.

SUBSECT. AUSTRALES

The 11 species of this group are now in eastern and southeastern North America. As based on genetic data resulting from numerous hybridization tries, Critchfield (1962) concluded that the group is a natural one. The few taxa that do not cross readily are either removed from the others by geographic distance or in "flowering" time.

The oldest fossils that may be allied to this group are the Paleocene *Pityostrobus* (*Pinus*) *lynni* (Berry) Miller (Berry, 1934; Miller, 1977b) and the Middle Miocene *P. collinsi* Berry (1936, 1941). Both are similar in external features to cones of *P. taeda* L. Miller (pers. comm., 1984) pointed out that *P. avonensis* Miller (1969), *P. buchananii* Underwood & Miller (1980), and *P. driftwoodensis* Stockey (1983) all belong to either *Australes* or *Ponderosae*, though it is not now possible to determine which one group they may represent. (see Stockey, 1984, table 1).

Species allied to Australes have been described from the Neogene of western Europe, including fossil pines similar to *P. taeda*, *P. pungens*, and *P. rigida* (Gaussen, 1960: 234). The illustrations generally resemble these pines, but a final decision must be based on a reexamination of the fossils themselves. That the records may represent species of Australes would be consistent with the Neogene record in western Europe, where many species allied to those now in the eastern United States occur. Among these are species of *Acer*, *Betula*, *Carya*, *Diospyros*, *Fagus*, *Hamamelis*, *Juglans*, *Lindera*, *Liquidambar*, *Nyssa*, *Persea*, and *Quercus*, as well as the conifer *Taxodium*. Some of them occur in intermediate areas, notably in the Miocene of Iceland (Akhmetiev et al., 1978; Heer, 1968; Moorbath et al., 1968). If *Australes* pines were in western Europe, they presumably were eliminated there along with the now-American hardwoods and swamp cypress during the later Pliocene and Pleistocene as cold and then ice spread southward. The presently-American (and Asian) taxa were blocked from southward retreat by the elevated Alpine axis that stretches across southern Europe and thus became extinct there.

SUBSECT. PONDEROSAE

Regarding the possible antiquity of this alliance, the recent description of well-preserved, silicified *Pinus* wood from the base of the early Upper Cretaceous Eutaw Formation (basal Coniacian), northeastern Mississippi, is of considerable interest (Blackwell, 1984). The wood is reported most similar to that of Subsect. *Ponderosae* (cf. *P. ponderosa*) though some of its features suggest relationship with woods of the allied Subsect. *Australes* (cf. *P. taeda*). *Pinuxylon eutawense* Blackwell may represent a pine ancestral to Subsect. *Australes*, or possibly to *Ponderosae* as well. In any event, yellow pines are clearly foreshadowed at this early date (ca. 88 Ma ago), as is indicated also by the cone of *Pityostrobus* (*Pinus*) *lynni* noted above.

Ponderosae fossils are certainly Eocene, as judged from seed-wing records and needles in

the Green River (MacGinitie, 1969) and Florissant floras (MacGinitie, 1953). In addition, needles of *P. andersonii* Stockey (1984), preserved in chert of the Allenby Formation (46 Ma) near Princeton, British Columbia, have the internal structure of *Ponderosae* needles. Furthermore, the silicified cone of *P. premurrayana* (Knowlton, 1899), from the east side of Yellowstone Lake, and probably from the early mid-Eocene Langford Formation (ca. 50 Ma, Smedes & Protska, 1972), is also a member of the *Ponderosae*. It is similar to cones of *P. lindleyii* Loudon, now in Mexico and considered by some to be a variety of *P. montezumae* (i.e., Martinez, 1948).

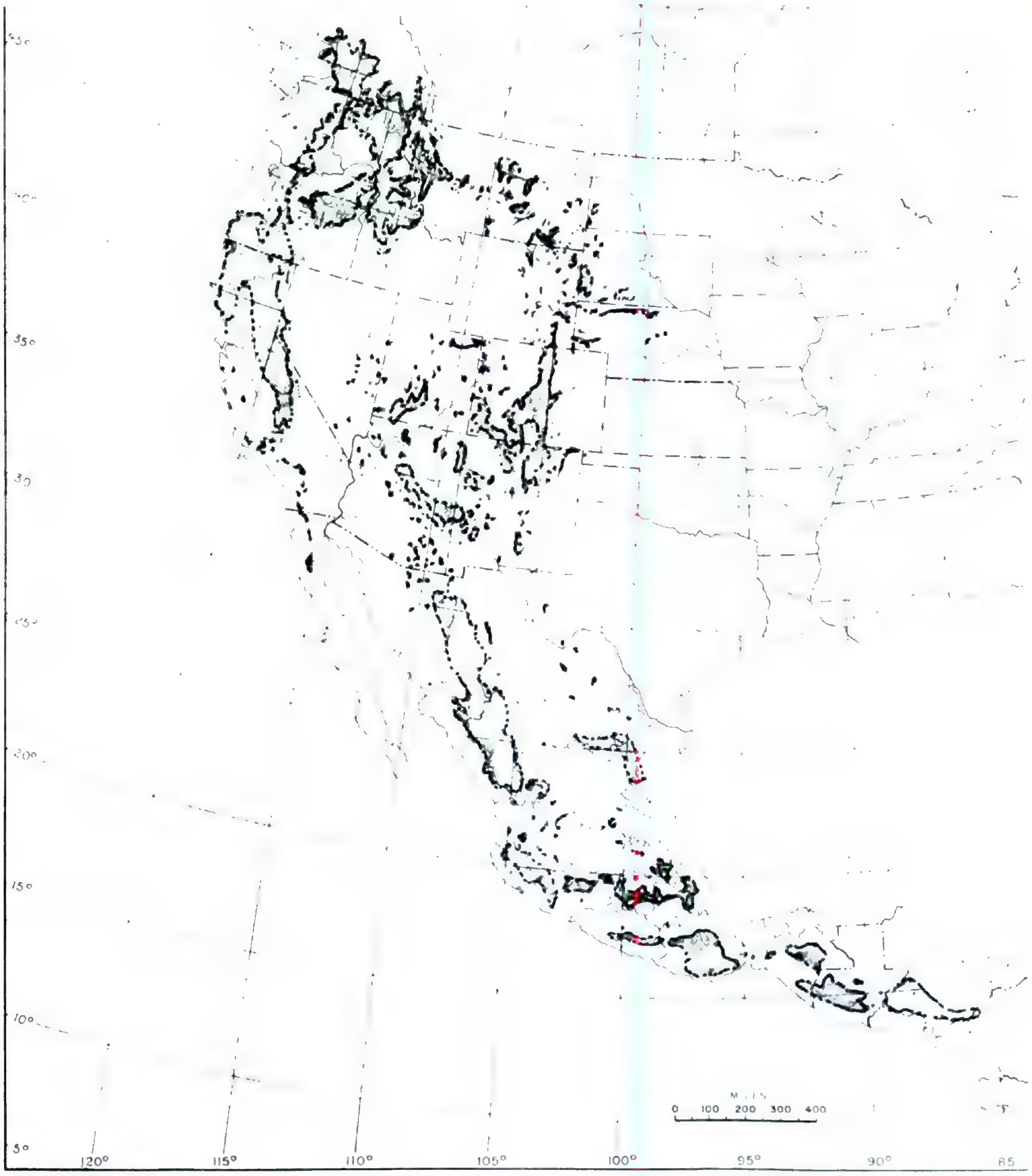
Remains of several *Ponderosae* are in the Late Oligocene Creede flora, Colorado. They resemble those of species now in the Southwest and/or Mexico, notably *P. chihuahuana, P. engelmannii, P. michoacana,* and *P. montezumae*. This suggests that the southern Cordilleran region that extended southward into Mexico was a major center for diversification of *Ponderosae* in the Paleogene. Its species probably were restricted southward gradually as colder climate spread over the central and southern Rocky Mountains, leaving *P. scopulorum* the chief survivor, and with *P. engelmannii* and *P. arizonica* reaching their northern limits in southern Arizona and adjacent New Mexico, a region of warmer climate (see Axelrod & Raven, 1985, figs. 5, 6). The remaining *Ponderosae* (e.g., *P. cooperi, P. douglasiana, P. durangensis, P. hartwegii, P. lawsonii, P. michoacana, P. montezumae, P. pseudostrobus, P. tecote*) now occur well south of the U.S.-Mexican border, or in California-Oregon (*P. jeffreyi, P. ponderosa, P. washoensis*).

A northwestward occurrence of a presently Mexican and Southwestern *Ponderosae* in the Miocene is indicated by *P. truckensis* Axelrod. It occurs in rocks 12.5 Ma old in the Truckee River drainage east of Reno, at Celetom diatomite quarry. The large asymmetrical cone is similar to those produced by *P. pseudostrobus*.

During the Middle and Late Miocene, branchlets, needles, and seed-wings similar to those produced by *P. ponderosa* occur at a number of sites in western Nevada, including the Eastgate, Fallon, Fingerrock, Middlegate, Stewart Spring, Pyramid, and Verdi floras. These are chiefly forest-border assemblages that lived for the most part under subhumid climate. By contrast, it is evident that *P. ponderosa*-like structures are largely absent in the floras of Oregon, Idaho, and Washington that occupied more humid climates.

Pinus ponderosa (including its varieties) has a broad range, reaching from southern British Columbia to San Luis Potosí, Mexico, a distance of 3,850 km (2,350 mi.). As noted by Critchfield and Little (1966: 16), it is absent from a large part of the intermontane region, notably southern Idaho, western Wyoming, southwestern Montana, and a good part of the Great Basin ranges of northern Utah and much of Nevada (Text-Fig. 16). However, fossil records show that *ponderosa*-like structures (needles, winged seeds) occurred in the region; the general rarity of fossils in the eastern part of the area reflects the fact that the rocks there are chiefly of Mesozoic and older formations.

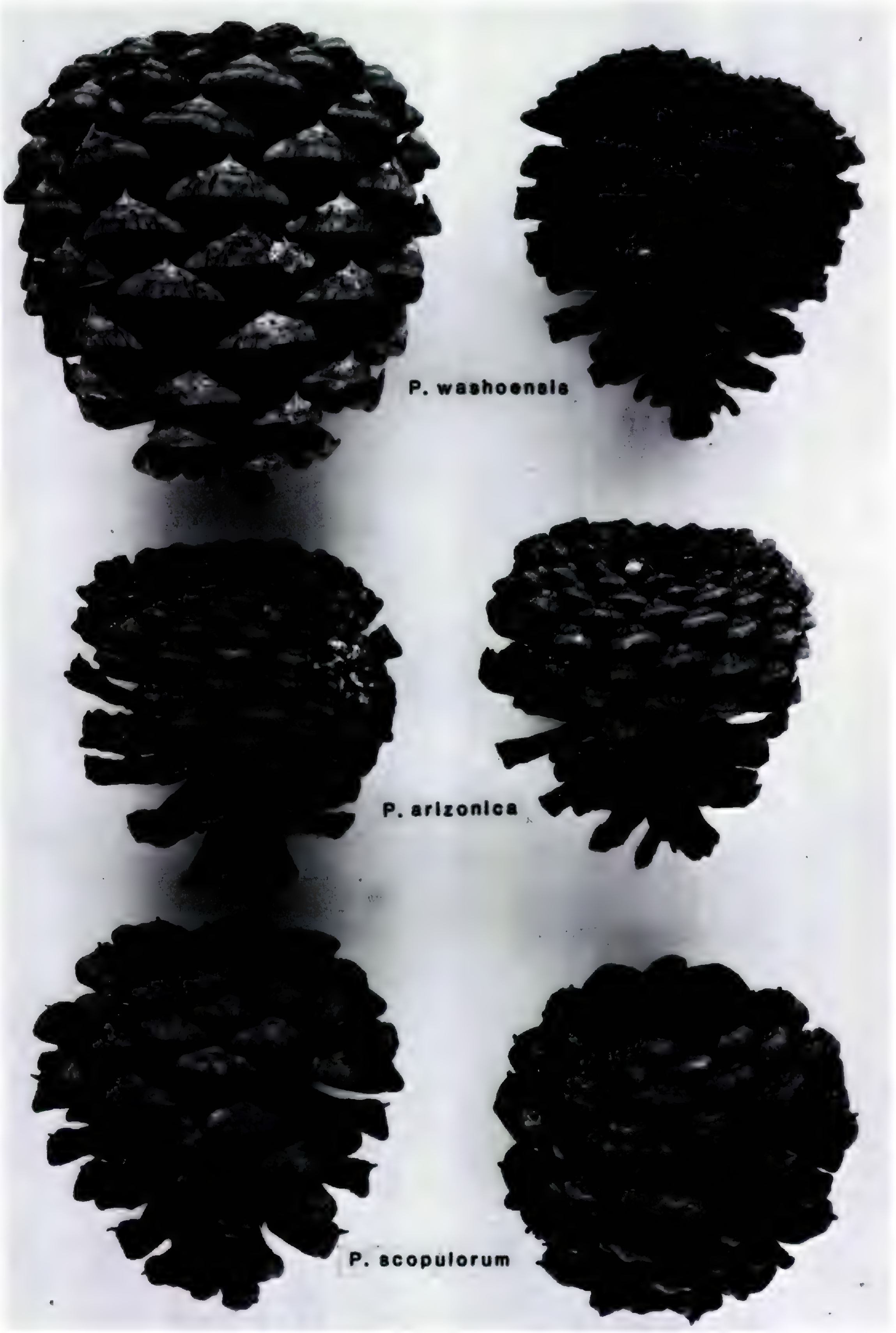
The present absence of *P. ponderosa* from much of the intermontane region may be explained by several factors (Axelrod, 1976a). In the first place, precipitation over most of the lowland region totals less than 250 cm (10 in.) and hence is insufficient to support these trees. The pine has a normal growing season from May through August. Since precipitation is low, seedlings cannot become established readily because adequate soil moisture is critical for establishment (Fowells, 1965). In this regard, *P. ponderosa* (*scopulorum*) does occur in the eastern Great Basin ranges, where late spring–summer rains are frequent. Pines that may have survived in the isolated ranges following the last glaciation probably were eliminated there by the post-glacial Xerothermic period. Increased summer evaporation rate would have been a critical factor in eliminating pine seedlings. Furthermore, trees probably could not survive by retreating upslope to moister areas because climate there is too cold in summer. In addition, aspen outcompetes pine in the same zone and may partly account for its absence over much of the region. An aspen-sage-meadowland association forms the zone in which pine would occur naturally (Axelrod, 1976a). Aspen competes with pine for water, but aspen, with its shallow, spreading roots, outcompetes pine seedlings. Aspen not only spreads rapidly by suckers in its early years (Fowells, 1965), it is also intolerant of shade, as is ponderosa pine. Hence, aspen competes further with pine seedlings if they are present. Under present conditions, the aspen-sage-meadowland zone is a relatively permanent drought-resistant vegetation type in the inter-



TEXT-FIGURE 16. Of the 12–13 species of Subsect. *Ponderosae*, only three occur north of southern Arizona (i.e., *P. ponderosa* with two vars., *P. jeffreyi*, *P. washoensis*). Note the broad area in the intermontane region where *ponderosa* does not now occur (see text for discussion).

montane region, occupying areas where *P. ponderosa* might exist if precipitation was higher.

The origin and relationships of *Pinus washoensis* Mason & Stockwell (1945) provide a noteworthy problem. The species occupies a continental climate and occurs in the upper mixed-conifer forest and in the fir forest. It is scattered discontinuously from the east slope of the Carson Range, Nevada, northward into British Columbia. The species is characterized by small, compact, ovate cones. Haller (1959, 1965, 1984) concluded that it is allied to populations of *P. ponderosa* ranging from the Lake Tahoe region northward through eastern Oregon into interior British Columbia. He noted that in its type area, where it is quite distinct, it only crosses with *P. ponderosa* with reduced seed set. It becomes less distinct northward and gradually tends to merge with the northern *P. ponderosa* populations. These hybrids are quite variable, suggesting that hybridization between the Rocky Mountain and Pacific races of *P. ponderosa* has played a role in


P. washoensis
P. arizonica
P. scopulorum

their origin. Haller concluded that *P. washoensis* may be a segregate from these hybrids maintained in isolation at the south, but only partially differentiated in the north where distribution is more continuous.

However, there appears to be evidence for its relict nature. This is implied by breeding studies that show that it crosses most readily with Rocky Mountain (Colorado-Black Hills) populations of *P. scopulorum* Engelm. and with which it produces most seeds (Critchfield, 1984a). Further, in terms of its seed proteins, the pine in its type area on Mount Rose has an antigenic distance of 0.6 from the Sierran ponderosa pine (Prager et al., 1976). This is greater than the distance between *P. jeffreyi* and *P. sabiniana* (0.4–0.5), although less than the values from *P. coulteri* and *P. engelmannii* (0.8–1.9) (Prager et al., 1976). The data presented by Critchfield (1984a) suggested that separation from an ancestral population may have occurred on the order of 20–30 Ma ago. This is possible since the remains of *P. ponderosa-scopulorum*-like pines occur in the Eocene and Oligocene. Critchfield also pointed out that in the ability of Washoe pine to cross with other taxa, it "behaves like a fragment of the Rocky Mountain race stranded at the west edge of the Great Basin."

To follow up this suggestion, I examined stands of *P. scopulorum* in eastern Nevada, western Utah, and southern to central Colorado and Arizona. In the last two areas, especially, the cones are generally similar to those produced by *P. washoensis* but are not so compact. They differ in that *P. scopulorum* cones are ovate, whereas those of *P. washoensis* are ovate-rotundate (i.e., rounded or globate), *P. washoensis* has more numerous scales (173 vs. 112–141); in cone color (purple vs. green for *P. scopulorum*); wing length (shorter vs. longer in *P. scopulorum*); and longer seeds in *P. washoensis* than *P. scopulorum* (Critchfield, 1984a).

Further evidence for a Cordilleran source for *P. washoensis* is provided by *P. arizonica* Engelm. of southern Arizona, adjacent New Mexico, and northern Mexico. This tree regularly produces small, compact, ovate-rotundate cones scarcely separable from those of *P. washoensis* (U.C. Herb. 335574, 334313—Santa Catalina Mts., 334316 Chiricahua Mts.; also see Shaw, 1909, pl. 17, fig. 4). The long needles are in fascicles of 3s and 5s, expectable in warmer regions where pines commonly have more needles (Shaw, 1914; Mirov, 1967). The similarities suggest that *P. washoensis* may have been derived from a population closely allied to *arizonica-scopulorum* (Text-Fig. 17). This implies that a population with generally small, globose cones ranged across the Great Basin during the Neogene. It may have originated during the later Middle Miocene (ca. 13–12 Ma) as climate rapidly became drier and numerous exotics disappeared from that region (Axelrod, 1985). Adaptation to increasing summer drought in the west presumably resulted in the development of somewhat more compact cones and shorter needles commonly in 3s, as seen in *P. washoensis*.

The suggestion that *P. washoensis* may be a relict population derived from a Cordilleran source is consistent with paleobotanical evidence. A number of basically Rocky Mountain and intermontane taxa now range across the Great Basin to the Sierra Nevada and border areas (see Little, 1971, 1976). Among these, the following have equivalent species in the Miocene floras from the present desert area of western Nevada:

Acer diffusum
Alnus tenuifolia
Amelanchier utahensis
Betula fontinalis
Celtis reticulata
Cercocarpus ledifolius
Elaeagnus velutina
Holodiscus dumosus
Juniperus osteosperma
Paxistima myrsinites
Peraphyllum ramosissimum
Pinus monophylla
Pinus ponderosa
Populus angustifolia
Prunus demissa
Prunus emarginata
Ribes cereum
Symphoricarpos oreophilus

Others with this distribution that do not now

←

TEXT-FIGURE 17. Cones of *Pinus washoensis* (from Mt. Rose, Nevada, alt. 2,430 m [8,000 ft.]), *P. arizonica* (from Huachuca Mts., Arizona, alt. 2,130 m [7,000 ft.] and *P. scopulorum* (from Creede, Colorado, alt. 2,675 m [8,800 ft.]) are so similar they indicate that these are closely related taxa. The suggestion that *P. washoensis* is a relict, Cordilleran taxon is supported by paleobotanic and genetic evidence (see text).

have a known fossil record in Nevada include *Chamaebatiaria millefolium, Pinus flexilis,* and *P. longaeva.*

Neogene floras of western Nevada, and also of central California, have a number of trees and shrubs allied to those in the southern Rocky Mountains, and some are represented by species only in Mexico. Among these are fossil species allied to:

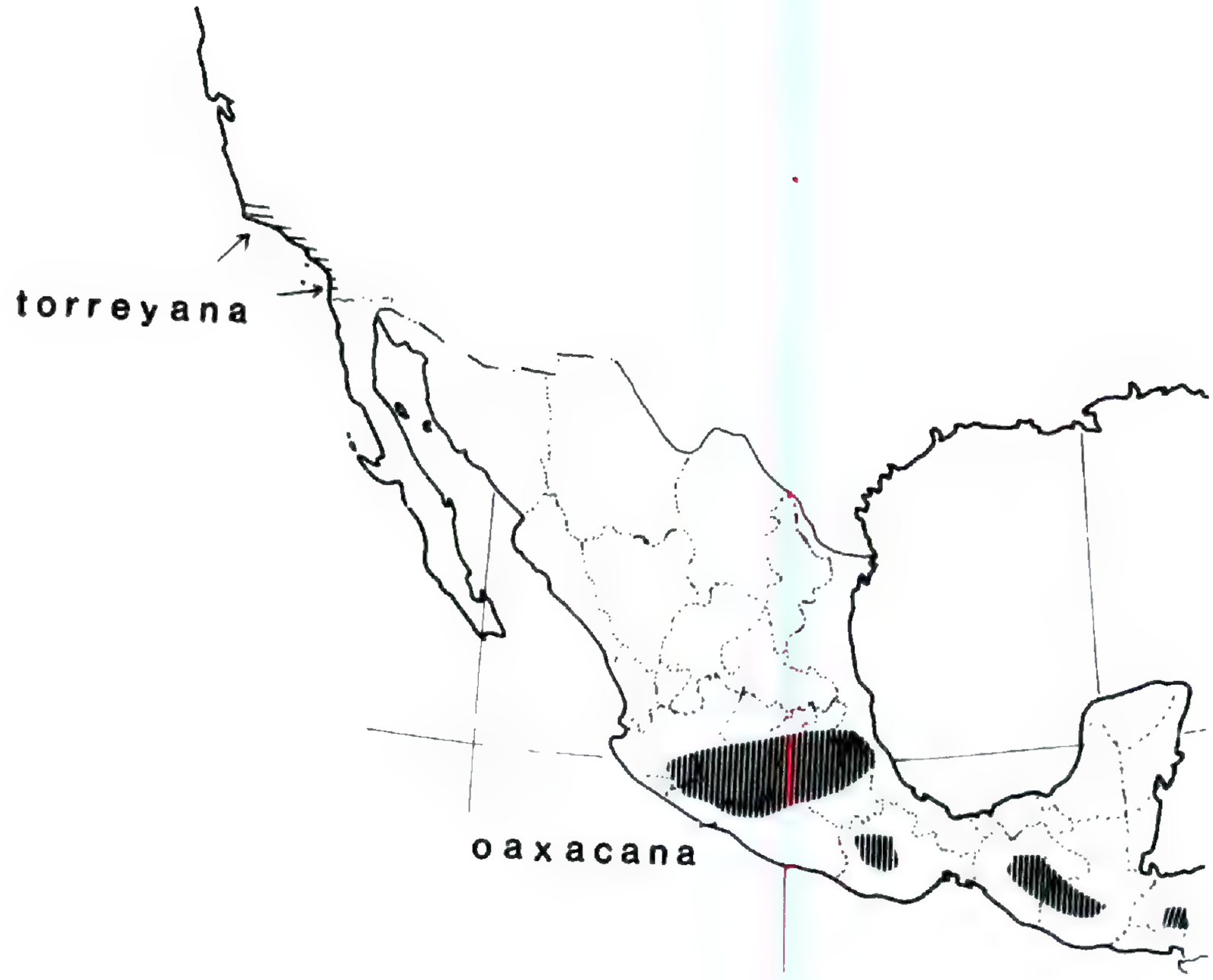
Acer grandidentatum
Arbutus arizonica
Bumelia lanuginosa
Cercocarpus breviflorus
Crataegus erythropoda
Fraxinus anomala
Juglans major
Populus brandegeeii
Populus mexicana
Quercus arizonica
Quercus vaseyana
Robinia neomexicana
Sapindus drummondii

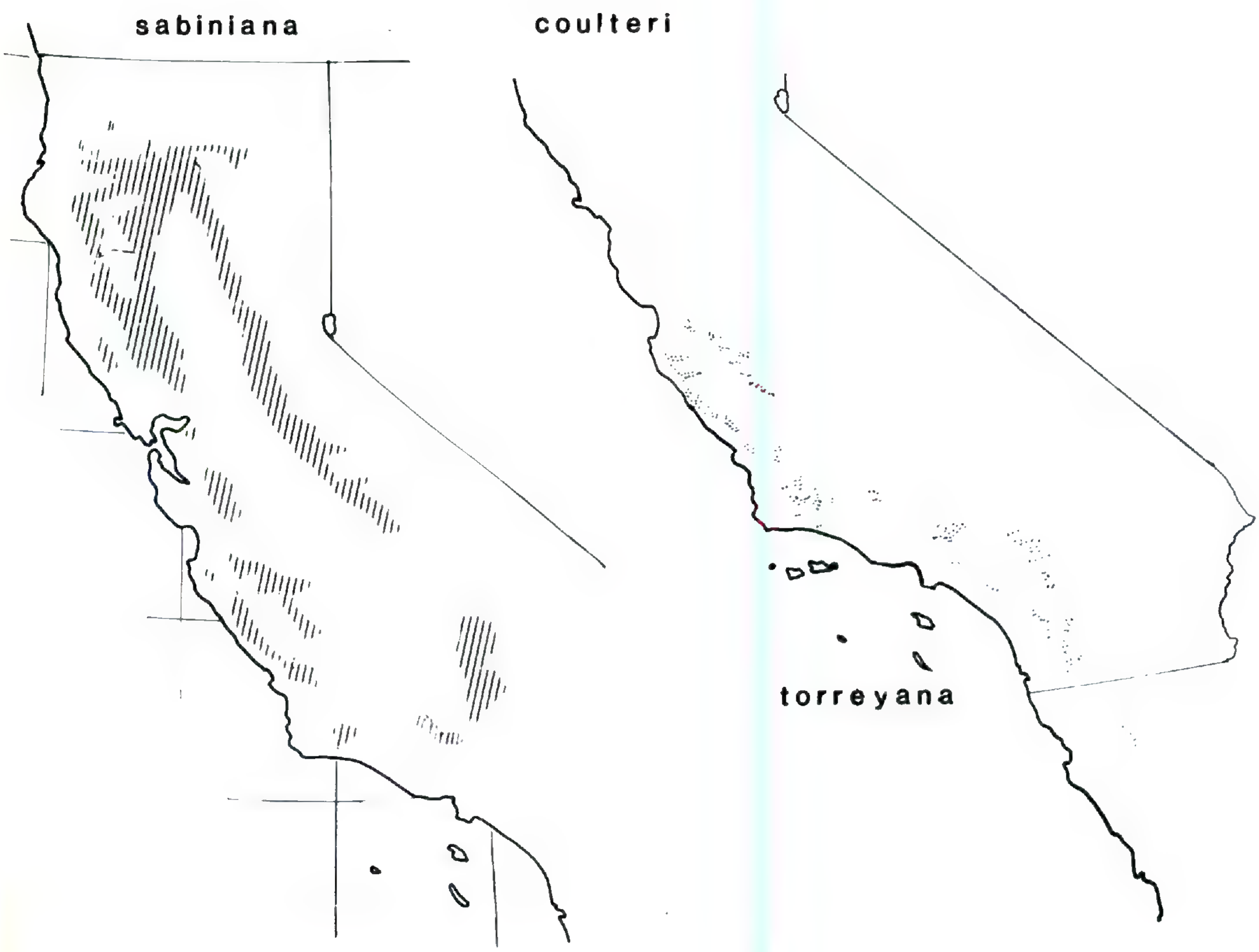
Fossil species of the above taxa contributed to mixed conifer forest, sclerophyll woodland, and juniper woodland, together with species allied to those now in California. The Cordilleran and Madrean taxa that occupied the present Great Basin during the later Miocene were largely eliminated there as summer rain decreased further in the Pliocene (Axelrod, 1976a). Relict stands occur now in the higher mountains bordering the eastern Great Basin where there is more summer precipitation, as well as along the eastern slope of the Sierra Nevada and bordering ranges where such typical "Rocky Mountain" taxa as *Pinus flexilis, Populus angustifolia,* and others still occur. In sum, the evidence seems compatible with the view that *P. washoensis* may be a relict Cordilleran pine, one derived from a plexus allied to *P. scopulorum* and *P. arizonica.*

SUBSECT. SABINIANAE

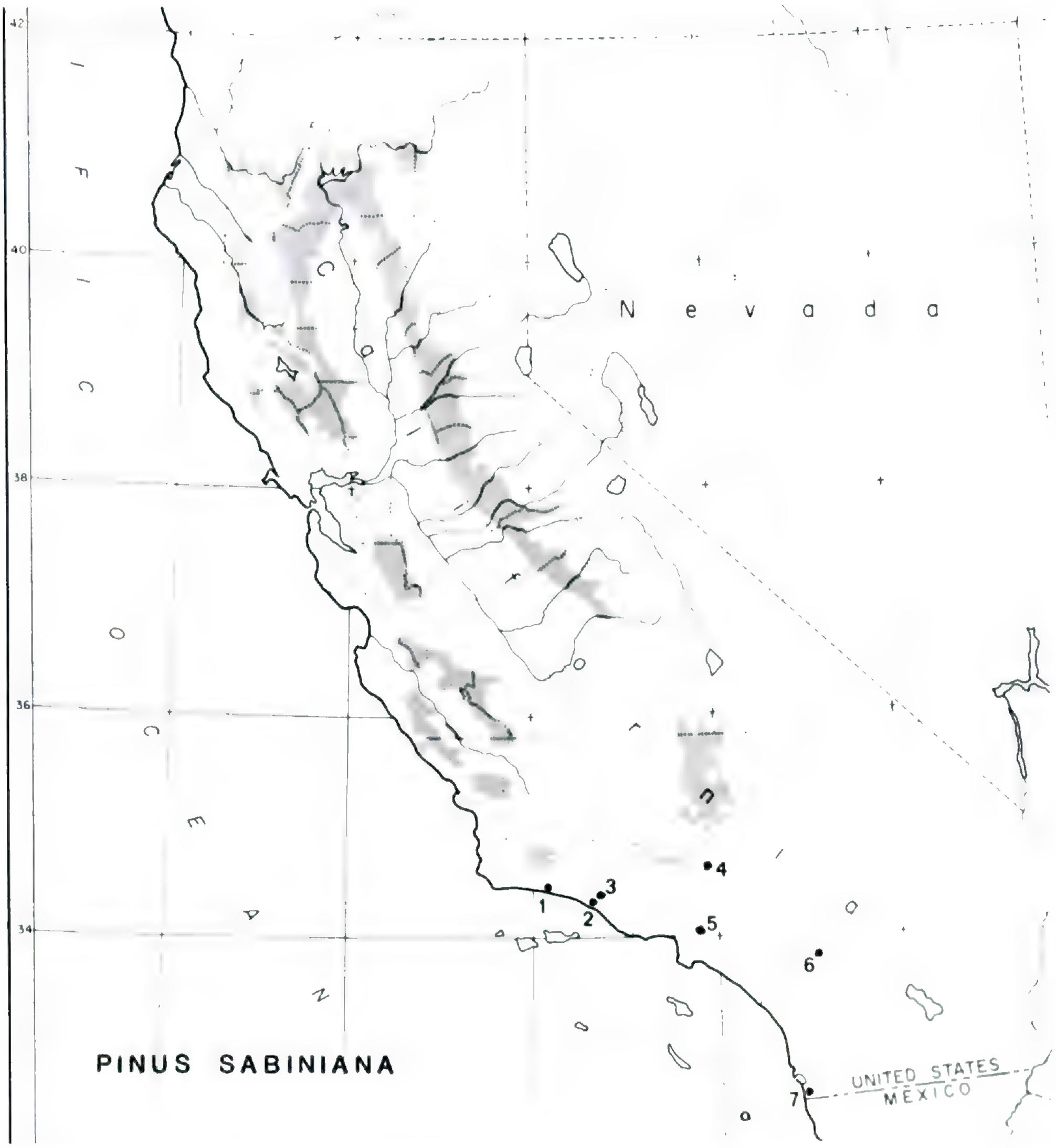
This small group of three pines, *P. torreyana, P. sabiniana,* and *P. coulteri,* occurs in California, with *P. coulteri* scattered discontinuously into the mountains of northern Baja California (Text-Fig. 18). The only species with a limited fossil record is *P. pieperi* Dorf, which is allied to, if not identical with, *P. sabiniana.* Confined now to the Coast Ranges and foothills of the Sierra Nevada in central and northern California, all of its fossil records are in southern California (Text-Fig. 19). These include the later Miocene Anaverde (Axelrod, 1950) and Mount Eden (Axelrod, 1937) floras, the Pliocene Chula Vista (Axelrod & DeMéré, 1984) and Pico (Dorf, 1930) floras, the Early Pleistocene Seacliff flora (Axelrod, 1983a), a cone from the Early Pleistocene in Lake Canyon near Ventura (Wiggins, 1951), and a cone scale in the late Pleistocene (Wisconsinian) Carpinteria (Chaney & Mason, 1933) and Rancho La Brea floras (Warter, 1976). *Pinus sabiniana* may have disappeared from southern California during the Xerothermic, which brought a hotter, semi-desert climate to the coastal strip. This climate may also account for the present disjunct occurrences of *P. sabiniana* in central and northern California, where isolated populations often are surrounded by mesic, mixed-conifer forest which spread with cooler, moister climate following the Xerothermic (Axelrod, 1966b: 50).

At present, there is no known fossil record of *Pinus torreyana,* one of the most restricted of pines. A few thousand trees now inhabit the coastal bluffs of Torrey Pines State Park and nearby Del Mar, a few miles north of San Diego, and a subspecies occurs on Santa Rosa Island, 60 km southwest of Santa Barbara (Haller, 1986). The mainland population is near the head of La Jolla submarine canyon. Upwelling of colder water gives this local area a foggier, cooler climate than the adjacent coast and may account for the persistence of *P. torreyana* there (Axelrod, 1982). There is also a highly marine, cooler, foggy climate on Santa Rosa Island. Cones of *P. torreyana* are similar to those of *P. oaxacana* Mirov of Mexico, a species that has long needles in 5s like *P. torreyana* (Text-Fig. 20). Significant in this regard is the occasional occurrence of strongly-hooked apophyses on cones of *P. oaxacana* that simulate those of the *Sabinianae* (specimens in Inst. Forest Genetics, Placerville, California). *Pinus torreyana* may have been derived from a *P. oaxacana*-like pine in western Mexico, which then extended west to include the present area of Baja California. Activation of the San Andreas rift system by the Early Miocene (or earlier?) transported the area, and the pine, northward (see Axelrod, 1980, figs. 7, 8). Fossil species allied to *P. sabiniana* and *P. coulteri* may have had a similar origin at the south but were adapted to interior lowland (*P. sabiniana*) and montane (*P. coulteri*) habitats. The difference in needles, which are more slender and drooping in *P. oaxacana,* and thicker and more rigid in *Sabinianae,* may reflect adaptation to the more xeric environment





TEXT-FIGURE 18. In Sect. *Pinus*, Subsect. *Sabinianae* has three species in California-Baja California, (*P. sabiniana*, chiefly in the interior at lower altitudes in central California; *P. coulteri*, montane in the inner Coast Ranges and southern California-Baja California, and *P. torreyana*, confined to two local areas in coastal southern California). Forerunner of the last may have been displaced northward from an ancestral population allied to *P. oaxacana* now in central to southern Mexico (see Text-Fig. 12).



TEXT-FIGURE 19. Fossil sites for *P. sabiniana* and its ancestor *P. pieperi* Dorf. (map from Griffin & Critchfield, 1972): 1—Carpinteria, 2—Pico, 3—Lake Canyon, 4—Anaverde, 5—Rancho La Brea, 6—Mount Eden, 7—Chula Vista. The species may have disappeared from southern California during the post-glacial Xerothermic period which brought hotter, drier conditions to the coastal strip.

in which the California taxa evolved. On this basis, records of fossil allies of the latter species are to be expected in the interior. A cone scale of a species allied to *P. sabiniana* occurs in the Miocene Anaverde flora of the western Mohave Desert (Axelrod, 1950). Its position 0.5 km west of the San Andreas fault is consistent with this thesis.

SUBSECT. CONTORTAE

Members of this alliance have been recorded in the late Eocene (38 Ma) Bull Run flora, northeastern Nevada (in Axelrod, 1968), the late Oligocene (26.5 Ma) Creede flora, Colorado (Axelrod, unpubl.), and the Early Miocene (21 Ma) Alvord Creek flora, southeastern Oregon (Axelrod, 1944). The first site is a rich montane conifer forest, the others are mixed conifer-hardwood forests. There is no evidence that *Contortae* were abundant in these floras. Their rise to prominence in the modern flora appears to be a later Cenozoic event, with rising mountains and spreading cold providing suitable environments for them, and with logging and fires, often set by man, aiding their rapid spread and crowding out of associated trees.

Pinus contorta var. *contorta* has a discontin-

uous distribution on the California coast from near Pt. Arena northward (Text-Fig. 21). This is probably a relict late Pleistocene occurrence, for the area has cool summers suited to its survival at the south. Its distribution is paralleled by *Picea sitchensis,* a species that ranged to Tomales Bay, 150 km farther south in the late Pleistocene (Mason, 1934). The var. *murrayana* of the Sierra-Cascade axis is discontinuous to the high mountains of southern California and Baja California (Text-Fig. 21). The latter sites are relict from the Early Quaternary (2 Ma), when mixed-conifer forest in interior southern California was fully 1,000 m lower in altitude (Axelrod, 1966b) and continuous with that in the Sierra Nevada. Later uplift of the Peninsular-Transverse ranges disrupted the earlier distribution of the mixed-conifer forest and accounts also for the disjunct occurrence of *P. contorta* var. *murrayana.*

The isolated *P. clausa* of Florida and nearby Alabama may have been derived from *P. virginiana* in the later Tertiary as climate cooled and a population was isolated at the south. Confined to dry (sandy) sites, it either escaped or survived competition of taxa in the rich, mixed-mesophytic forest of the region during the climatic fluctuations of the Quaternary.

SUBSECT. OOCARPAE

Fossils of this group are presently known from California, Nevada, and Oregon in the west, and from Massachusetts in the east. Some of these are certainly extinct. *Pinus tiptoniana* Chaney & Axelrod (1959) from eastern Oregon appears allied to species like *P. patula* and *P. pringlei* as judged from its umbo relationships. *Pinus burtii* Miller (1978) from Martha's Vineyard, Massachusetts, is a large-coned species that may be distantly related to the *P. radiata* complex. This is suggested by the large, rounded apophyses, although the cone appears more nearly symmetrical. *Pinus burtii* provides a link with the upland flora of central Mexico where other members of the *Oocarpae* now occur. Continuity with the pines of Mexico is certainly old and probably is Late Eocene-Early Oligocene. Recall that the Late Eocene (35 Ma) Barilla flora of trans-Pecos Texas (Berry, 1919) represents a rich palm-laurel forest in this now semi-desert area. Furthermore, the Appalachians already supported an Eocene temperate deciduous forest as judged from the pollen record (Gray, 1960), and the inner lowlands of the Gulf Coast were covered with a rich, warm temperate forest with many taxa now in Mexico (Fredericksen, 1980, 1981). A warmer, milder climate is indicated also by the Miocene Legler flora (11 Ma) in the Cohansey Formation, New Jersey (Greller & Rachele, 1983). It has several genera (e.g., *Cyathea, Podocarpus, Engelhardtia*) now in the mountains of eastern Mexico, under wet, equable climate.

At present, numerous species and varieties of trees and shrubs are common to the temperate forest of the uplands of eastern Mexico and the eastern United States (Harshberger, 1911; Axelrod, 1939: 78; 1960: 267–268; Graham, 1973). A corridor via the Appalachians-Ozarks-trans-Pecos Texas and into Mexico in the Late Eocene-Early Oligocene may account for these ancient, surviving links, and suggests stasis for these taxa extends back fully 30–25 Ma. Elimination of species of present temperate Mexican occurrence from the eastern United States resulted from the trend to less equable climate later in the Cenozoic, and especially in the Pleistocene. It also eliminated many subtropical broadleaved evergreens, leaving the present impoverished deciduous hardwood forest with a few evergreen dicotyledons confined chiefly to the milder coastal strip, as exemplified by *Gordonia, Ilex, Magnolia, Persea,* and *Quercus* (*Q. virginiana, Q. laurifolia*).

Members of the *Oocarpae* now in California include three species in the coastal area (*P. remorata, P. radiata, P. muricata*) and one (*P. attenuata*) in the interior and in southwest Oregon (Vogl et al., 1977). The nearest affinities of *P. radiata* and *P. remorata* are with *P. oocarpa,* now in Mexico. *Pinus oocarpa* has cones very similar to those of *P. remorata* and to the small-coned *P. radiata* var. *cedrosensis* of Cedros Island and *P. radiata* var. *binata* of Guadalupe Island (Axelrod, 1980; Text-Fig. 22). Evidence suggests that the *Oocarpae* now in maritime California were displaced northward as terrain west of the San Andreas rift zone moved to its present area (Text-Fig. 23). This was from an earlier position that placed southern California at the latitude of Sonora, with the Cape Region of Baja California nestled near Cabo Corrientes, Jalisco (see Text-Fig. 12). The *P. radiata* populations on islands off Baja California (*P. radiata* vars. *cedrosensis* and *binata*) may be relicts of that distribution. In addition, a number of trees and shrubs associated with the *Oocarpae* in coastal southern California and northern Baja, California (e.g., near Eréndira) also appear to be remnants of that movement. These include narrow endemics that find their nearest allies in the mountains of Mex-

TEXT-FIGURE 20. Cones of *Pinus torreyana* are similar to those of *P. oaxacana*. In addition, both have long needles in 5s and large sheaths. The fossil forerunner of *torreyana* may have been was displaced northward by movement on the San Andreas fault system during the Miocene and later (see Text-Fig. 12).

ico where they are also associated with *Oocarpae*. Examples are in paired-species of *Arbutus, Ceanothus, Cercocarpus, Comarostaphylis, Myrica, Pinus, Prunus* (*Laurocerasus*), *Quercus,* and *Vaccinium* (Axelrod, 1967b).

With respect to evolution of the *P. radiata* series, the var. *cedrosensis* appears to simulate the most ancient member of the alliance for its cones are very similar to those of *P. oocarpa*. A *P. radiata* var. *cedrosensis*-like population presumably gave rise to the Guadalupe Island *P. radiata* var. *binata*. The latter appears to have been ancestral to the California populations (Text-Fig. 24). Its cones range from those with apophyses scarcely developed (like *P. radiata* var. *cedrosensis* and *P. remorata*) to those that are inseparable from cones of the Monterey population. Similar variation occurs in cones recovered from the Pliocene San Diego Formation at Chula Vista, which places the insular *P. radiata* var. *binata* on the mainland (Axelrod & DeMéré, 1984).

As land area west of the San Andreas and allied rifts moved north, climate there was becoming progressively drier in summer in response to cold-water upwelling along the coast. As summer rains decreased further, and the mediterranean-type

TEXT-FIGURE 21. Distribution of three varieties of *Pinus contorta* today (map from Little, 1971). The southernmost sites for coastal *P. contorta* var. *contorta* evidently were attained in the Late Wisconsin. The occurrence of *P. contorta* var. *murrayana* in southern and Baja California apparently dates from the early Quaternary (2 Ma) when forest taxa lived about 1,000 m lower than they do today (Axelrod, 1966).

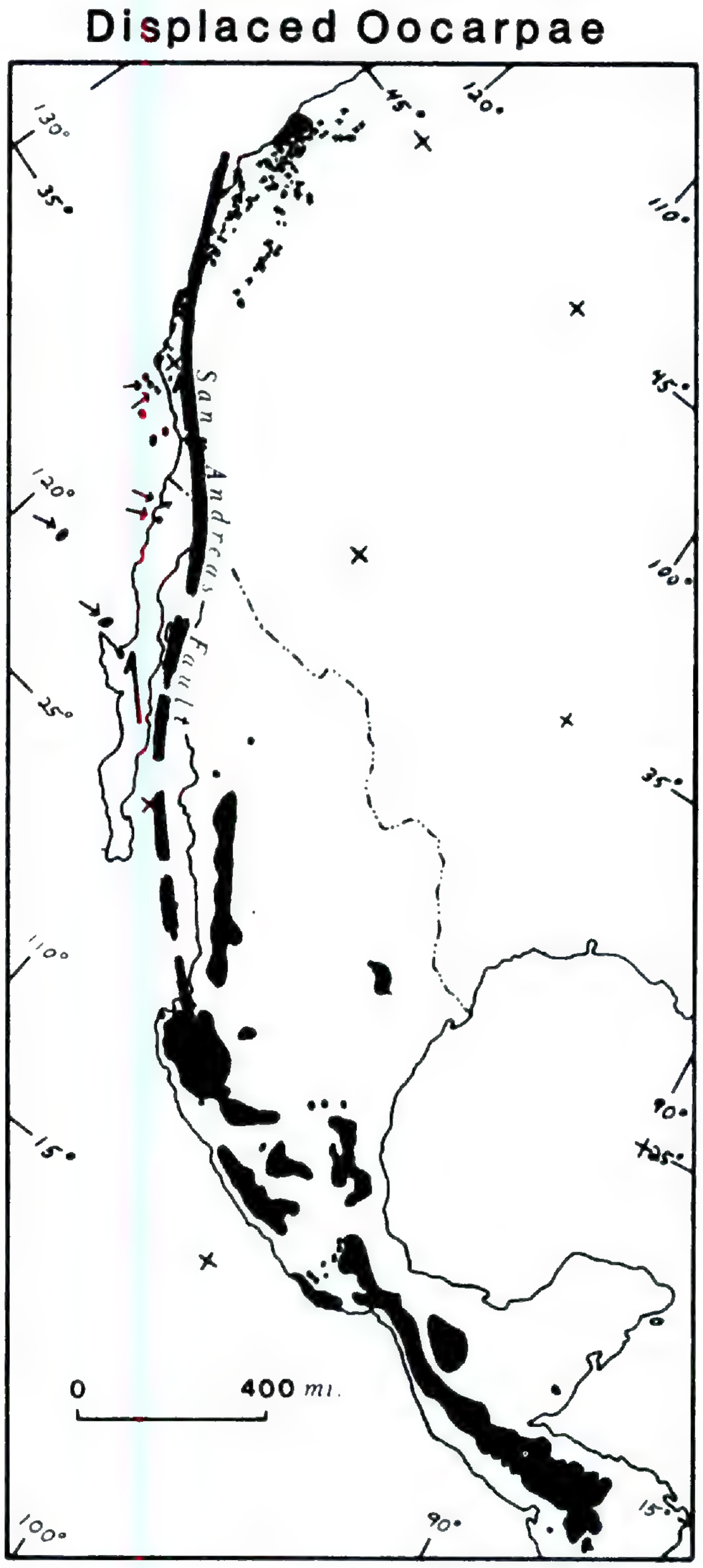
climate became more intense, cones of the three California populations evidently increased in size and also developed larger apophyses and seeds. The population at Monterey-Carmel has smaller cones than the stands 70 km northwest at Año Nuevo or 135 km southeast at Cambria (Text-Fig. 25). This apparently reflects survival of an older population in the cooler, foggier climate at Monterey. It results from the influence of the Monterey submarine canyon on local climate there, an area where two cypresses (*Cupressus macrocarpa, C. goveniana*) also have relict occurrences, as do a number of shrubs and forbs (Axelrod, 1982).

TEXT-FIGURE 22. Cones of four closely related pines of Subsect. *Oocarpae, P. oocarpa, P. remorata,* and *P. radiata* vars. *cedrosensis* and *binata.*

Pinus radiata, P. muricata, and *P. remorata* all had wider occurrences in coastal California in the Late Pleistocene (Axelrod, 1967a, 1967b). *Pinus radiata* evidently formed a nearly continuous forest from near Inverness, 60 km northwest of San Francisco (Axelrod, 1976a, 1980), to Chula Vista near San Diego (Text-Fig. 26), some 825 km southeast (Axelrod & DeMéré, 1984). The record of *P. muricata* is not so complete, but it certainly had a wider occurrence, for the northern population *P. muricata* var. *borealis* reached south at least to the Santa Barbara area. *Pinus remorata* also occurred more widely than at present. Restriction of these taxa to local areas today is chiefly the result of the warmer, drier, post-glacial climate, and especially that of the Xerothermic, which disrupted the more mesic forests. The present relict populations survive chiefly in areas of favorable, local climate where cold-water upwelling gives those areas a cooler climate with a high fog frequency. A similar relation exists at Eréndira, Baja California, where *P. remorata* and *P. muricata* occur in a semi-desert climate bordering an ocean that is much colder and foggier in this local area (Axelrod, 1982).

The other member of the *Oocarpae* in California is *P. attenuata,* confined chiefly to interior regions, generally at the lower margin of mixed-conifer forest. It is most nearly allied to the Mexican *P. greggii, P. patula,* and *P. pringlei,* although the cones of *P. attenuata* are more strongly armed. The fossil *P. pretuberculata* may have spread northward from an ancestral, interior plexus and then been stranded in California as developing arid climate to the south disrupted its connection with the Mexican taxa (Axelrod, 1979). In this respect, the isolated *P. attenuata* population east of Ensenada has cones somewhat intermediate in shape to those of central Mexican species.

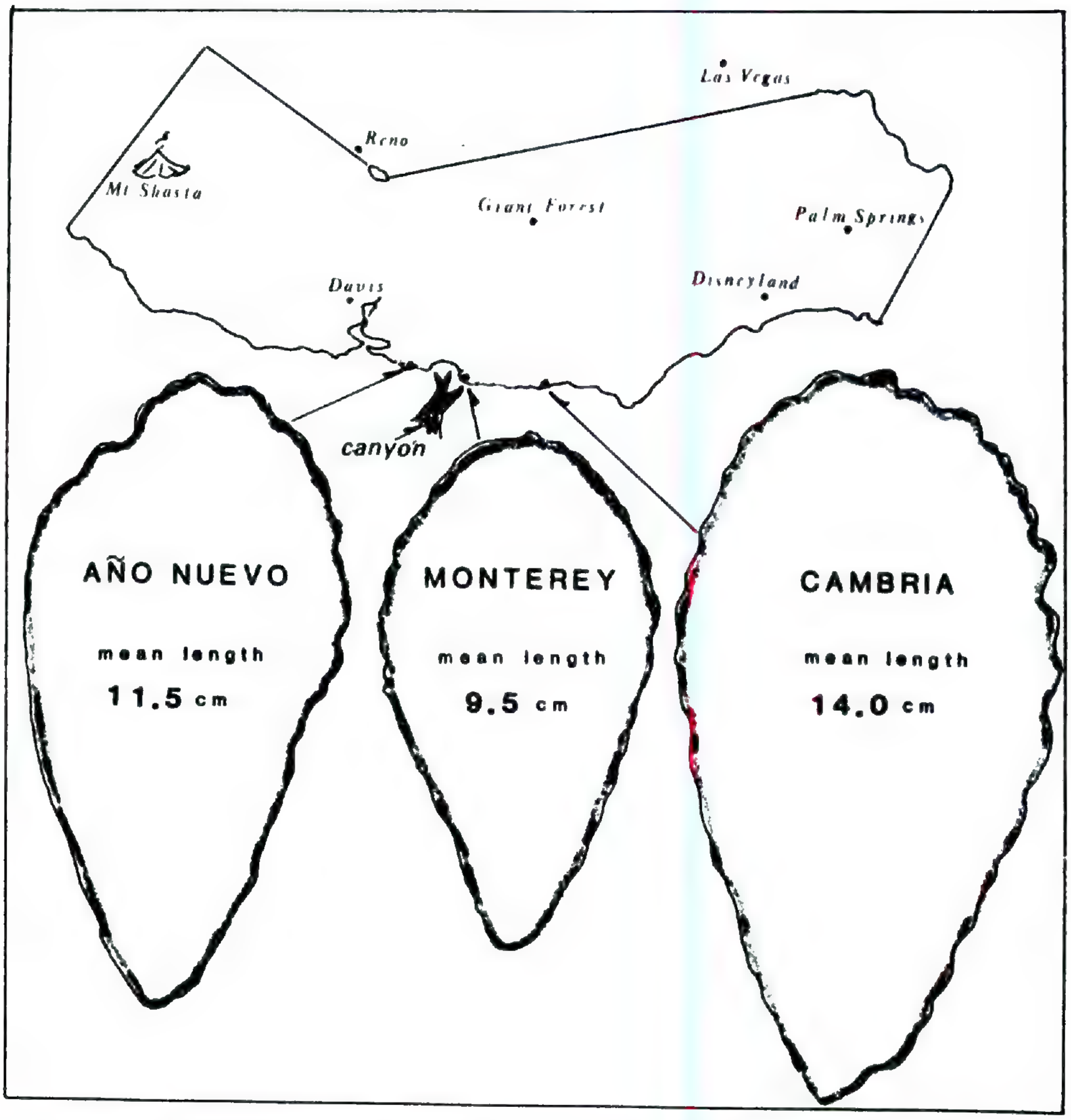
The fossil *P. pretuberculata,* which is very similar to cones of *P. attenuata,* was already in California in the Upper Miocene (12 Ma) Table Mountain flora (Condit, 1944). It is recorded from youngest Miocene rocks (5–6 Ma) in the Mount Eden flora of southern California (Axelrod, 1937) and the Verdi of western Nevada (Axelrod, 1958). *Pinus attenuata* is also in Early Pleistocene rocks at Signal Hill (Mason, 1932) and Seacliff (Axelrod, 1983), coastal southern California. At these latter sites, the cones probably were transported from the interior. This is likely because *P. at-*



TEXT-FIGURE 23. Distribution of species of *Oocarpae,* with four species each in California-Baja California (*P. attenuata, P. muricata, P. radiata, P. remorata*) and Mexico (*P. greggii, P. oocarpa, P. patula, P. pringleii*). (Map from Critchfield & Little, 1966.) The taxa in coastal California-Baja California evidently were displaced northward by movement on the San Andreas rift system (see Text-Fig. 12), as were other taxa whose nearest allies are now in Mexico (see text). Spreading desert climate further isolated these taxa.

TEXT-FIGURE 24. Variation in cones of *P. radiata* var. *binata* suggests that it may have been ancestral to the present California populations. This inference is consistent with the occurrence of Pliocene cones at Chula Vista, southern California, similar to those of var. *binata*. Increasing summer drought in California evidently resulted in the trend to larger cones and seeds.

tenuata occurs at these sites with closed-cone pines (*P. muricata, P. radiata*) that require humid, equable climate, whereas *P. attenuata* regularly inhabits drier sites away from the coastal lowlands, in more extreme climates of the interior. The species is restricted now to isolated stands in southern California, on the crest of the Santa Ana Mountains, and in the San Bernardino



TEXT-FIGURE. 25. The California populations of *P. radiata* have larger cones and apophyses than do the Mexican populations from Cedros and Guadalupe islands. Although the larger cones appear to represent a response to increasing summer drought in California, note that the Monterey population has smaller cones than do populations at Año Nuevo and Cambria to the north and south. This reflects the position of the Monterey population opposite Monterey submarine canyon, where cold water upwelling makes the Monterey area the foggiest part of the coastal strip. Thus protected from spreading drought, the small-coned, probably ancestral, Monterey population has survived there with other relict endemics (from Axelrod, 1982).

Mountains. These local ocurrences, as well as the relict population east of Ensenada, may have resulted from restriction during the Xerothermic, when semi-desert taxa moved coastward from the interior and forests retreated upslope.

A unique Late Pleistocene occurrence is provided by a cone of *P. attenuata* recovered from an excavation at Oakland, on the east side of San Francisco Bay (Metcalf, 1923). Today the nearest stand is east of the Oakland Hills, some 12 km distant, where climate is hotter in summer and colder in winter. The pine evidently extended west to Oakland in a Late Pleistocene glacial age when sea level was about 100 m lower and the shoreline was fully 50 km (30 mi.) farther west (Helley & LaJoie, 1979). Climate was then more continental in the San Francisco Bay trough, which was dry land, as shown also by mammoth and other mammals recovered there during dredging. With the rise of sea level, and the return of milder, oceanic climate, the Oakland *P. attenuata* population disappeared, leaving survivors in the interior. A few interior species that still have rare populations in the Bay area probably are also relicts of the drier, Xerothermic climate (Axelrod, 1981).

LATE CENOZOIC EVOLUTION

Into the middle Tertiary many trees (probably most) of temperate regions had comparatively wide distributions that resulted from low environmental diversity. Climates were broadly zoned, they were highly equable, and more aseasonal in lower latitudes. Furthermore, terrain differences were not so marked as those of today.

TEXT-FIGURE 26. *Pinus radiata* occurs today at: A—Ano Nuevo, B—Monterey-Carmel, C—Cambria, D—Guadalupe I., and E—Cedros I. Fossil localities for Monterey pines occur at: 1—Tomales Bay, 2—Drakes Bay, 3—Thornton Beach, 4—Mussel Rock, 5—Spring Valley Lake, 6—Little Sur, 7—Pt. Sal, 8—Carpinteria, 9—Seacliff, 10—Pico, 11—Potrero Canyon, 12—Rancho La Brea, 13—Mount Eden, 14—Chula Vista, 15—Santa Rosa I. Disruption of the Late Pleistocene forest probably resulted from spreading Xerothermic climate that brought hotter, drier interior conditions to the coastal strip. The present relict stands are all confined to local areas of high fog frequency during summer.

High continuous ranges like the Sierra Nevada-Cascades or the Rocky Mountains, and high plateaus (Colorado Plateau, Mexican Plateau) had not yet come into existence. As regional topoclimatic differences developed later in the Cenozoic, the stage was set, especially in Mexico, for the rapid splitting of populations into new races, varieties, and probably some species.

Apart from geographic (spatial) and ecologic (edaphic) differences, isolation of populations may also result from seasonal climatic differences that determine times of major reproductive events (Stebbins, 1950: 208–209). This is seen notably in the co-occurrence at Monterey of *Pinus radiata* and *P. muricata,* which do not form hybrids because of fully two months difference in maturation of microsporangia. A similar separation is seen in the populations of *P. radiata* and *P. attenuata* at Swanton and Año Nuevo, north of Monterey. Differences in time of "flowering" that isolate populations may account for different populations (or varieties) of piñon (*P. cembroides*) recently described from the Southwest and Mexico. Most live under subhumid to marginally semiarid climates and are spread across 23° of latitude, or 2,800 km (1,775 mi.). Times of pollination vary greatly across this broad region depending on local climates (warmth), which are the result of recent tectonism that formed the ranges and basins in which these populations now occur. A similar explanation may also apply to *Pinus ponderosa,* which releases pollen at very different times of the year in British Columbia, Utah, California, and San Luis Potosí at its southern occurrence. These regional differences may have been a factor in the rise of varied races in these areas of very different rainfall and temperature regimes (adaptive subzones), and times of pollen shedding.

The closely similar species of *Strobi* that extend more or less continuously from the Canadian Rockies in British Columbia southward through the Sierra Madre Occidental into Guatemala, may also be considered in this context. There is a transition zone between *P. flexilis* and *P. strobiformis* and between *P. strobiformis* and *P. ayacahuite.* The shift from one species to the next occurs in areas of major topographic-climate change. These are along the Colorado-New Mexico border, and in the transition from central Arizona-New Mexico southward where climate rapidly becomes warmer (Axelrod & Raven, 1983), and in central Mexico, with warmer conditions farther south where *P. ayacahuite* occurs. The climatic differences, which determine time of pollen maturation, dispersal, and fertilization, have been intensified in the later Cenozoic. Natural hybrids of these species regularly occur in these transition zones.

Pines now in boreal regions and subalpine areas that form pure stands are subject to very low temperatures in winter. The most extreme are those in the area of *P. pumila* in northeast Siberia. Mean January temperature is −47.6°C (−52°F) at Verkhoyansk and −43.2°C (−45°F) at Yakutsk. Summers are sufficiently warm in these areas for boreal forest, with a mean July temperature of 16°C (60°F) at Verkhoyansk and 19°C (66°F) at Yakutsk. These extreme conditions developed recently, chiefly in the Quaternary. In the Middle Miocene (ca. 15 Ma) the area of northeast Siberia was covered with a rich conifer-deciduous hardwood forest much like that now on the middle mountain slopes from central Honshu to southern Hokkaido. This is apparent from the flora of Mammoth Mountain on the Aldan River (Dorofeev, 1969), about 200 km northeast of Yakutsk. It includes species of *Abies, Larix, Pinus, Acer, Betula, Broussonetia, Corylus, Cornus, Juglans, Morus, Padus, Prunus, Pterocarya, Salix,* and several others. Comparable Miocene floras are known also from Kamchatka (Menner, 1976), Sakhalin (Heer, 1878a, 1878b), Iceland (Heer, 1868), and Alaska (Heer, 1869). The shift to colder climate was largely post 5–6 Ma, as polar climates spread and mountains were elevated to alpine levels. This enabled subalpine and boreal conifers to form more continuous populations as hardwoods were eliminated by progressively increasing cold. During the later Tertiary, these northern coniferous populations adapted to more severe conditions by physiological shutdown (see discussion in Axelrod, 1983b: 126–128). This does not mean that pure conifer forests were not present until the later Tertiary—they were. The Eocene Upper Bull Run flora of northeastern Nevada is wholly dominated by conifers at seven sites distributed stratigraphically through fully 1,160 m (3,500 ft.). The conifers include species of *Abies, Larix, Picea, Pinus, Tsuga,* and *Chamaecyparis.* The only dicotyledons are a few shrubs distributed in *Crataegus, Holodiscus, Mahonia, Malus, Prunus, Ribes,* and *Salix.* This Upper Bull Run flora succeeded a mixed conifer-hardwood forest after 38 Ma as climates became colder (Fig. 2). If pure stands of pine (i.e., species of *Cembrae, Strobi, Balfourianae*) contributed to subalpine forests,

they must have occupied slopes fully 500 m or more above the rich (15 taxa) montane conifer forest of the Bull Run basin.

A contributory role in the development of conifers, as well as vascular plants, has been played by mycorrhizal fungi, as discussed by Malloch et al. (1980). Pines have ectomycorrhizae, those in which the fungus surrounds the living cell of the root and does not penetrate it. The mycorrhizae extend out into the soil and serve to transfer nutrients from decaying litter into the plant from generally nutrient-poor soils. The mycobionts are very diverse in ectotropic forests, whereas the photobionts often form nearly pure, monotonous stands, as in the boreal and subalpine forests of colder regions (Malloch et al., 1980). Today, ectotropic forests like the boreal forest may commence on new sites with various dicotyledonous species, but the conifers become increasingly dominant. They may reach an equilibrium state that enables the best-adapted species to form forests of considerable stability (Meyer, 1973: 88). However, this is a new regional relationship, for pure conifer forests are not recorded as widespread, zonal vegetation types in the Tertiary. The available record in western North America indicates that they were restricted mostly to localized, higher and colder altitudes (see Axelrod, 1968; 1976a). Pure pine forests spread in response to increasing cold (*P. banksiana, P. contorta, P. cembra, P. pumila*), or drought (*P. cembroides, P. monophylla, P. edulis, P. ponderosa*), or to seasonality. As noted above, these are new environmental conditions in terms of forest history, whether in North America or Eurasia. Thus, the mycorrhizae have given Pinaceae, and *Pinus* in particular, an adaptive edge as environments have become more extreme, whether in cold regions, the seasonal tropics, or in edaphically unique areas (sandy sites, acid soils, etc.). The numerous pine species in Mexico occupy areas of seasonal climate and often poor soils. Many of these sites are on well-drained and effectively drier volcanic and carbonate rocks and hence are favorable sites for pines. These areas largely resulted from relatively recent volcanism or tectonism, which uplifted and exposed older rock units, often carbonates. With the presence of ectotrophic mycorrhizae in abundance, as well as seasonal climate affecting time of pollen shedding, fluctuating climate in the late Cenozoic, and more recently disturbance by man (fires, clearing), it is understandable that pines were able to form pure stands and many new races and varieties in the Mexican uplands and border areas.

The Quaternary changes noted above are further illuminated by a current paper by Critchfield (1984b) that considers the impact of Pleistocene climatic changes on the genetic structure and distribution of North American conifers, notably some species of *Abies, Picea,* and others. His interpretations are based on evidence from fossil pollen records, wood-rat middens, glacial and inter-glacial megafossil floras, and isoenzyme and terpene analyses of living conifers. In northern areas, the data provide evidence for population retreat during glacial times and their spread from refugia in post-glacial times. Over western areas, the record reveals the wider distribution of conifer species over lowlands presently desert and semidesert during the pluvials, as well as the occurrence of presently high montane conifers at altitudes fully 900–1,000 m lower. As Critchfield concluded, the most general effect has been the evolution and extinction of transitory races of boreal conifers, and, in some western conifers, the rise of longer-lived races through repeated cycles of isolation and hybridization. The influence of climatic fluctuations thus involved extinction of some species and races, the nearly complete loss of genetic variation in others, and occasional gene enrichment through hybridization and introgression.

FUTURE WORK

Discovery of new fossil ovulate pinaceous cones (*Pityostrobus, Pinus*) will no doubt further illuminate pine history. This will be particularly effective if large collections can be obtained, especially in older montane basins, or at higher latitudes, areas where Tertiary pines are more abundant. A most critical need, however, is the discovery of Tertiary floras in the Mexican uplands, a prime area of pine evolution. Comparisons of fossil taxa with species of modern subsections are necessary if we are to do more than merely describe new taxa.

Biochemical studies (isozymes, terpenes, DNA analysis) of modern species may provide evidence to estimate relative age of taxa. This would be of high interest for, in contrast to fossil species that have already developed their characteristics, the data may provide indications of the time of divergence of allied taxa. This could shed light

on the age of presumably paired-taxa on different continents (*P. griffithii-P. monticola, P. cembra-P. albicaulis*) and in different parts of one continent (*P. strobus-monticola, P. edulis-monophylla*).

Continuing hybridization studies of modern species of the subsections may aid in further understanding species interrelationships.

Conclusions

The preceding review suggests that pines have been opportunistic throughout their history. They appear to have adapted early to generally stressful areas and probably originated there. Their evolutionary success probably was favored by their symbiotic relationship with ectotrophic mycorrhizae. This enabled them to inhabit drier sites, areas of seasonal rainfall, poor edaphic conditions (sand, laterite, podsol), and, late in their history, very cold regions. Pines responded rapidly on several occasions to increased topographic, climatic, and edaphic diversity by splitting into alliances ("subsections") of different adaptive mode. They have radiated into mountains in temperate and tropical regions, they inhabit dry areas at the lower limit of tree growth (*P. monophylla, P. ponderosa, P. sabiniana*), they have reached into extremely cold regions at timberline (*P. albicaulis, P. aristata*), at tree-line in boreal regions (*P. banksiana, P. pumila*), and others have entered seasonally dry tropical areas with leached soils (*P. cubensis, P. dalatensis*). More recently, pines have formed pure stands in colder (*P. banksiana*) and drier (*P. cembroides, P. ponderosa*) regions as older, richer forests and woodlands lost taxa and retreated to more favorable areas as climate changed. That pines are still opportunistic is evident in the uplands of Mexico for evolution is active there, as seen in the variation in *P. cembroides, P. montezumae, P. oocarpa, P. pseudostrobus,* and others. As on earlier occasions in pine history, Mexican pines recently responded to the rapid appearance of new environments—created there by volcanism, tectonism, new local climates, and fluctuating climate—to form new races and varieties by hybridization and introgression. Although pines are indeed ancient, they are highly successful. In terms of sheer numbers of individuals, there are more pines today than at any time in the past 140 million years, and they also wholly dominate vegetation over broad regions—a recent event.

PART 2. SYSTEMATICS

When George Englemann's *Revision of the Genus Pinus* was published in 1880, scarcely any fossil pines were then known from North America. A few had been described by Heer (1868–1882) from the high arctic and were assembled later in his six-volume classic, *Flora Fossilis Arctica.* Secured by various expeditions, the collections were small and inadequate, and the pines are represented chiefly by imprints of fragmentary needles, winged seeds, and a few broken cones. They are associated with taxa that contributed to deciduous-hardwood and conifer-hardwood forests of Paleocene, Eocene (Ellesmere I., Spitzbergen), and Miocene (Kamchatka, Sakhalin, Iceland, Alaska) age. In the volume describing the *Geological Exploration of the Western Territories,* Lesquereux (1878, 1883) reported on fossil floras from a number of localities in the western United States. Most of these represent vegetation of humid, warm temperate to subtropical environments, climates in which pines are largely absent. The early explorations of western Canada disclosed several small fossil floras in British Columbia and areas to the north (Dawson, 1883, 1890, 1891; Penhallow, 1908). They also contained scrappy remains of conifers, notably needles, winged seeds, and broken cones of pines and other conifers.

As more detailed geological studies of local areas proceeded during the decades following the 1920s, fossil floras were recovered from more numerous localities, and those from moderate altitudes often included remains of pines. Some of these, like the Copper Basin and Bull Run floras of northern Nevada, are in structural (fault) basins. Others, like the Creede of Colorado, the Hermosa of New Mexico, and the Thunder Mountain of Idaho, are preserved in sedimentary deposits that accumulated in the moats of large calderas that developed from collapse following explosive volcanism.

Although a century has elapsed since the early collections were made, our knowledge of pine history is still in a very preliminary state. This reflects the fact that there are relatively few good collections of fossil pines. Furthermore, since only a few investigators have been interested in the group, our understanding of pine history has been impeded further. In this review of previously-described as well as new Tertiary pines, attention is centered on the external form of cones pre-

TABLE 2. Tertiary ovuliferous *Pinus* cones with described internal structure.

Species	Structure	Occurrence and Age	Apparent Affinity
Pinus avonensis Miller (1969)	Cone	Near Avon, Montana, Oligocene	Subgenus *Pinus* (9 subsections)
Pinus arnoldii Miller (1973; Stockey, 1984)	Cone	Allenby Fm., B.C., Middle Eocene	*Sylvestres*
Pinus wolfei Miller (1974)	Cone	Cowlitz Fm., Wash., Late Eocene	*Contortae, Oocarpae, Sylvestres*
Pinus burtii Miller (1978)	Cone	Miocene Greensand, Martha's Vineyard, Miocene	*Oocarpae*
Pinus buchananii Underwood & Miller (1980)	Cone	Twin Bridges Fm., Wash., Oligocene	*Australes, Ponderosae*
Pinus escalentensis Banks et al., 1981	Cone	Escalente Fm., B.C., Oligocene	Sect. *Pinus* (6 subsections)
Pinus driftwoodensis Stockey (1983)		Driftwood Creek Beds, B.C., Middle Eocene	*Australes*
Pinus princetonensis Stockey (1984)	Cone	Allenby Fm., B.C., Middle Eocene	*Sylvestres*
Pinus similkameenensis Miller (1973)	Fascicle, 5s	Similkameen beds, B.C., Middle Eocene	*Strobus*
Pinus similkameenensis Miller (1973), Stockey (1984)	Wood	Similkameen beds, B.C., Middle Eocene	*Parrya*
Pinus allisonii Stockey (1984)	Fascicle, 2s	Allenby Fm., B.C., Middle Eocene	*Sylvestres*
Pinus andersonii Stockey (1984)	Fascicle, 3s	Allenby Fm., B.C., Middle Eocene	*Ponderosae*

served as imprints in fine-grained sedimentary rocks because the external characteristics of fossil cones are similar to living pines. Less emphasis is placed on isolated winged seeds and fascicles of needles because most cannot readily be assigned to species groups.

As discussed by Miller (1976), and Banks et al. (1981), cones of *Pinus* have four main features. Species of *Pityostrobus* may possess some, but not all of these: 1) ovuliferous scales inflated at apex, 2) vascular supply to bract-scale complex leaves axial cylinder as a single unit, 3) resin canals in the base of the scale are abaxial to the scale trace, and 4) the vascular bundles in the distal part of the scale are rounded on their adaxial side (Text-Fig. 1). While these differences may separate most Cretaceous and some Paleogene cones of *Pityostrobus* from those of *Pinus, Pityostrobus* cones certainly are pinaceous (Miller, 1976, table 2). Since fossil ovulate cones acknowledged to represent *Pinus* were already present in the Early Cretaceous (ca. 120–125 Ma) (Alvin, 1960), *Pityostrobus* species apparently represent surviving members of an older plexus from which *Pinus* had diverged by the latest Jurassic. Inasmuch as *Pityostrobus* has been recorded only once in the Paleocene (Miller, 1977b), it presumably largely became extinct in the Cretaceous-Tertiary transition, and was replaced by *Pinus*.

Studies of the internal structure of permineralized *Pinus* cones from older Tertiary rocks have not greatly clarified their relationships within the subsections (Table 2). Most of the described species have been compared with one or two subsections, yet cones of species in these alliances may differ considerably in external features (form; apophyses; umbo-mucro position, etc.). The diversity of cone types within these groups, as well as the megafossil record of external impressions, implies that a number of species in the subsections were already in existence in the Eocene (see below). One of the problems raised by studies of internal structure of fossil cones is that the external form of the cones and its features (apophyses, umbo-mucro) are not always available for analysis. Some described fossil cones are so incomplete, owing to erosion or decomposition prior to burial, that their external characteristics have been erased (e.g., *P. wolfeii, P. avonensis*), and the form of others, if preserved, was not illustrated or described prior to sectioning.

In view of the preliminary stage in our knowledge of American Tertiary pines, it is desirable to clarify the approach to systematics followed here. Since most fossil pine taxa are based on

disassociated structures (cones, needles, winged seeds) at a given locality, these are grouped into species that appear to represent one taxon. In this way, a plethora of names that might otherwise be used is eliminated, and some semblance of biotic relationship can be suggested. For example, a cone of *Pinus* in the Late Eocene Bull Run flora is allied to *P. contorta*. Also in the flora are winged seeds that fall within the range of variation shown by that alliance. Seeds similar to those produced by *P. contorta* are in the Creede flora, Colorado. All this material is referred to the previously-described *P. alvordensis* Axelrod, which is a winged seed of the *P. contorta* alliance. It is granted that the fossils from these sites may represent different species of Subsect. *Contortae*. However, at this stage in our understanding of pine history, and in view of the limited sample, it seems best to group them into one fossil taxon, for the fossils can scarcely be separated taxonomically. A second example is provided by *Pinus crossii* Knowlton, based on fascicles of 5s in the Creede flora, Colorado. My large collections from 15 sites in the Creede Formation show that short needles in 5s are abundant at most sites. There are fossil cones and winged seeds in the flora similar to those produced by the living *P. aristata*, a species that has short needles in 5s. Rather than describe the cones and winged seeds as two additional species in the Creede flora, all of this material is referred to *Pinus crossii*, a species allied to *P. aristata*.

Identification of the fossils in this report has been based chiefly on comparisons with the large collection of modern pine material at the Institute of Forest Genetics, Placerville, California. This has made it possible to suggest relationships between the fossils and modern taxa, and hence to assign the fossils to subsections. It is emphasized that comparison of a fossil pine with a modern species does not mean that the living taxon has persisted unchanged from the Eocene or Oligocene down to the present. The comparison simply means that, as judged from what actually is available, a particular living species is most nearly related to the fossil pine which is given a separate name.

In the following discussion of some Tertiary pines, emphasis is on the imprints of fossil cones, for this is their usual mode of occurrence. Analysis of their modern relationships is aided by reference to the umbo-mucro features of the cone scale presented by Klaus (1980). Furthermore, appraisal of the affinities of cone imprints commonly is aided by making latex casts of the mold. In addition, the relationships of cones may be clarified by associated fascicles and winged seeds.

The Little and Critchfield (1969) system of classification followed here divides the genus into three subgenera, four sections, and 15 subsections (Table 2). The distribution of the modern species is well illustrated by Critchfield and Little (1966).

Subgenus Strobus

Sect. Strobus

Subsect. *Strobi*

This subsection includes six American and eight Eurasian species that occur chiefly in relatively mesic, mixed-conifer and conifer-hardwood forests. The close similarity between the American *P. monticola-strobus* and the Eurasian *P. peuce-parviflora-griffithii* pines is noteworthy. Future studies of their seed protein composition may indicate the times of separation of these allied species on each continent, and those that are now on separate land areas.

Although several species of Subsect. *Strobi* are on each continent today, there is no clear evidence that presently American species were represented earlier by similar species in Eurasia, or vice versa. The report that *Pinus monticola* var. *fossilis* (Sukachev, 1910) from the Pliocene of Siberia is similar to the present American *P. monticola* (Mirov, 1967: 56; Wolfe & Leopold, 1967: 199) is incorrect. The illustration shows that the cone differs from those of *P. monticola* in being more robust, is not so slender when closed (in water), and the cone scales are larger and thicker than those of *P. monticola*. The fossil is more nearly allied to present Asian species, notably *P. armandii* Franch. of central China. A similar, but more complete, cone of *P. itelmenorum* is in the Mammoth Mountain flora on the Aldan River (Dorofeev, 1969). Its more massive size and broader, thicker scales show that it is allied to *P. armandii* and its relatives, not to *P. monticola*.

Pinus anthrarivus Axelrod, sp. nov. TYPE: U.S.A. Idaho: Coal Creek. U.C. Mus. Pal., holotype 7165, paratypes 7166–69, 7218–20. Figures 1–5.

Needles in 5s, 4–6 cm long, very slender, averaging 0.5 mm broad; tips very acute; sheath deciduous. Winged seeds 1.5–2.5 cm long, seed ovate to oval, rounded distally, apex rounded to

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blunt, wing widest near middle, distal end broadly rounded.

Discussion. The scores of fascicles in the Coal Creek flora with slender needles at first suggested relationship with *P. strobus,* rather than *P. monticola,* which has thicker needles. However, the winged seeds differ markedly from the slender wings with acute tips produced by those species. In general shape they are more nearly allied to species of *Groupo Ayacahuite* (Martinez, 1948), and especially to the seeds of *P. ayacahuite* var. *veitchii* Shaw. *Pinus anthrarivus* thus appears to be an ancient member of Subsect. *Strobi,* one showing relationship to present Mexican species of the *ayacahuite* complex.

A radiometric date indicates that the pine and associated flora is 29 Ma old, or Late Oligocene.

Pinus delmarensis Axelrod, sp. nov. TYPE: U.S.A. California: Del Mar. U.C. Mus. Pal., holotype 7170. Figure 6.

Cone closed owing to immersion in water; cone long-cylindrical; 26 cm long (estim.), 6 cm broad; cone scales thin, 3+ cm wide in middle of cone, flat to broadly concave, no evidence of pronounced reflexing; scales apparently with terminal umbos.

Discussion. This cone from the Del Mar Formation, a few miles north of San Diego, is associated with sediments that yield both a molluscan fauna (Hanna, 1926) and vertebrate fauna (Golz, 1976) of Middle Eocene age, approximately 46 Ma old.

The cone is so similar to those of *P. lambertiana* there is no ready basis for separating them. In view of the fragmentary nature and rarity of all presently-known specimens of this alliance, it seems best to tentatively consider that the species is different than *P. prelambertiana* Axelrod from the Late Tertiary. The record suggests that *P. delmarensis* may have been separated geographically from a complex that included forerunners of *P. strobiformis* Engelm. and *P. ayacahuite* Ehrenberg as California west of the San Adreas shifted north following the early Miocene.

The presence of higher relief in the region to the east is indicated by coarse conglomerates in the associated section and by the spore-pollen flora (Frederiksen et al., 1983). In particular, the presence of pine pollen allied to the *Ponderosae* and *Strobi* groups indicates that terrain in the interior probably was near 1,300–1,500 mm, whereas the coastal strip was covered with a dry tropical flora.

Pinus florissantii Lesquereux, Rept. U.S. Geol. Surv. Terr 8: 138, pl. 21, fig. 13, 1883. Florissant, Colorado. Princeton Univ. Paleobot. Coll. holotype 144. Figures 8, 9.

Pinus florissantii Lesquereux. MacGinitie, Carnegie Inst. Wash. Publ. 599: 84, pl. 19, fig. 2, 1953.
Pinus similis Knowlton, U.S. Geol. Surv. Prof. Paper 131-G, p. 186, pl. 41, figs. 12, 13, 1923.
Pinus wheeleri Cockerell. MacGinitie, ibid., p. 85, pl. 18, fig. 11 only, 1953.
Pinus leaves, MacGinitie, ibid., pl. 18, fig. 3, 1953.

Pinus similis Knowlton was based on two fascicles of four needles in the Creede flora. Many additional fascicles have now been collected, and it is evident that most are in 5s, but some are in 4s and, more rarely, in 3s. The last are probably the result of needle loss during ageing or transport. The suite of *P. similis* foliage from Creede is similar to that produced by the modern *P. flexilis* James, and is therefore placed in synonymy under *P. florissantii* Lesquereux, based on a cone similar to those produced by *flexilis* today.

Supplementary description. Fascicles mostly in 5s, some in 4s; needles 4.0–5.2 cm long, 1.0 mm wide, stout and mostly curved; margins entire, prominent stomatal bands; tip acute; sheath absent, the proximal end forming a rounded (globose) area.

Discussion. Knowlton made no suggestion as to the identity of the Creede foliage referred here to *P. florissantii.* Comparison with western members of the *Strobi* shows that it is most similar to foliage of *P. flexilis* James; fascicles of *P. monticola* are generally not so robust. *Pinus flexilis* is a regular member of the mixed-conifer forest of the central and northern Rocky Mountains. It is discontinuous across the central Great Basin to the east slope of the central and southern Sierra

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FIGURES 1–7.—1–5. *Pinus anthrarivus* Axelrod, sp. nov. Coal Creek, Idaho. U.C. Mus. Pal., holotype 7167, paratypes 7165, 7166 (needles), 7168, 7169 (seeds). Late Oligocene, 27 Ma.—6. *Pinus delmarensis* Axelrod, sp. nov. Del Mar Formation, California. U.C. Mus. Pal., holotype 7170. Middle Eocene, 48 Ma.—7. *Pinus prelambertiana* Axelrod. Vedder Sandstone, California. U.C. Mus. Pal., hypotype 7171. Lower Miocene, 23 Ma.

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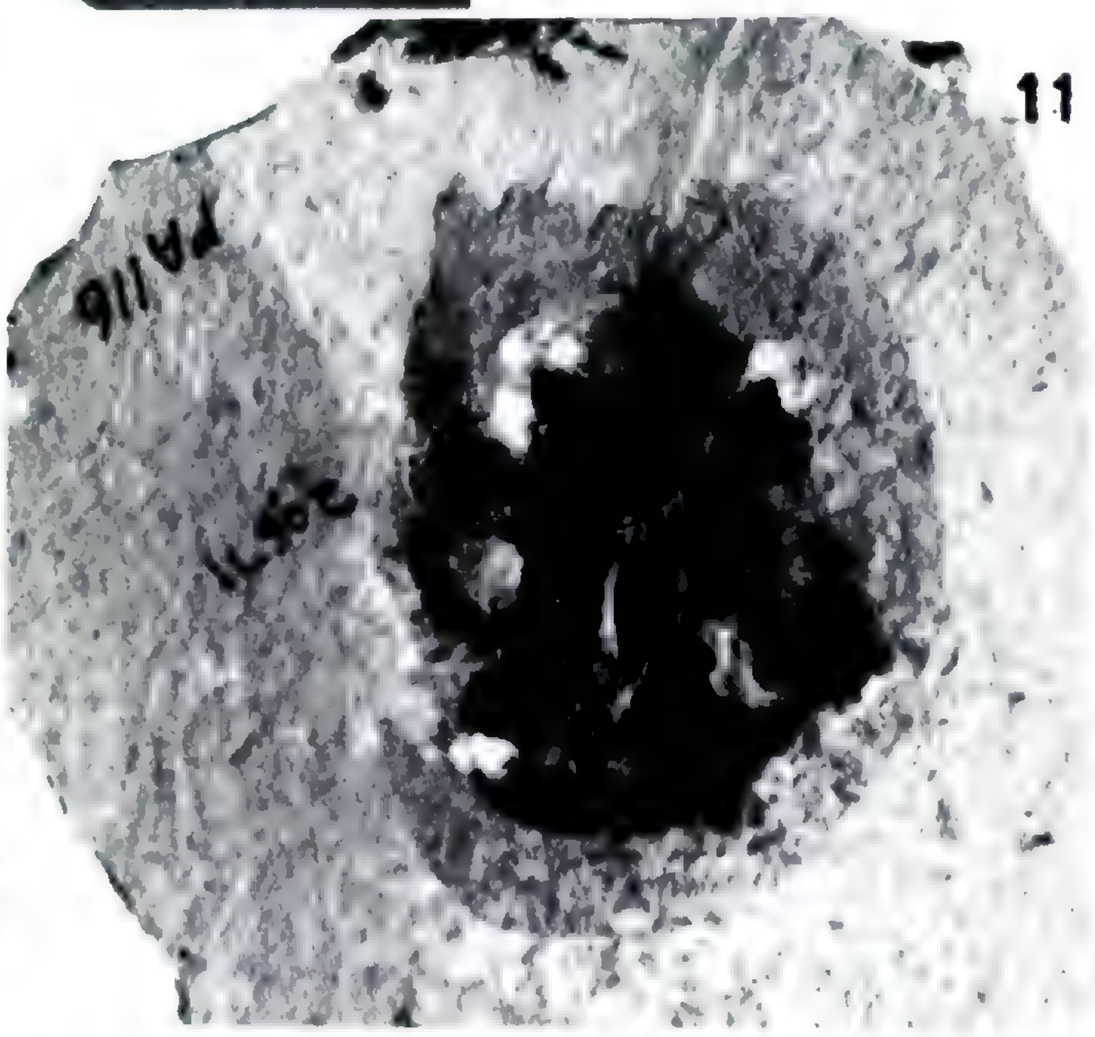
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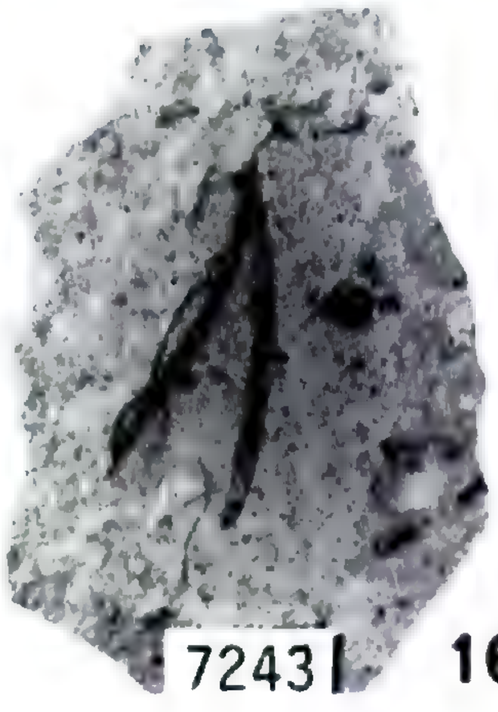

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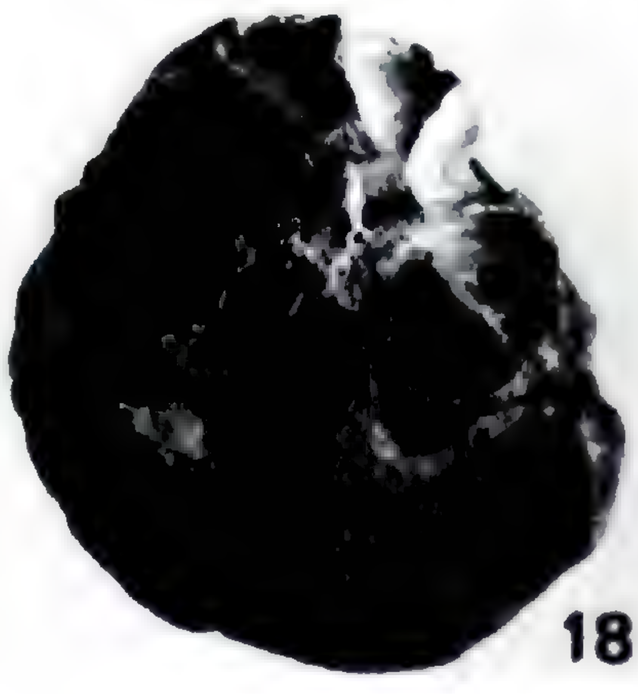
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Nevada, ranging southward in the Peninsular Ranges to the Santa Rosa Mountains, southern California.

The Florissant flora is well dated at 34 Ma, or earliest Oligocene (Epis & Chapin, 1975: 48).

Occurrence. Florissant, Colorado: U.C. Mus. Pal., hypotypes 3727, 3775; Creede, Colorado: U.C. Mus. Pal., hypotype 7214, homeotypes 7212, 7213.

Pinus prelambertiana Axelrod, Carnegie Inst. Wash. Publ. 412: 71, pl. 6, fig. 1, 1930. Santa Clara, California. U.C. Mus. Pal., holotype 309. Figure 7.

Pinus prelambertiana Axelrod, Univ. Calif. Publ. Geol. Sci. 24: 127, pl. 18, figs. 7–10, 1958.

The figured cone is from the Lower Miocene Vedder Sandstone at Pyramid Hill, northeast of Bakersfield, California. Vedder Sandstone is in the *Turritella inezana* zone and in the microfossil Zemorrian Stage, both of earliest Miocene age, 25–26 Ma (Turner, 1970).

Discussion. The cone is similar to those produced by *P. lambertiana* Douglas. The record indicates that in the Sierra Nevada to the east, climate was sufficiently moist and cool to support conifers. With ample summer rain and a more equable climate, the forest no doubt occurred at a lower altitude than the modern forest where *P. lambertiana* is confined now to altitudes above 1,300–1,500 mm.

Occurrence. Verdi, Nevada: U.C. Mus. Pal., hypotypes 1976–1978; Vedder Sandstone, California: U.C. Mus. Pal., hypotype 7171, homeotype 7172.

SECT. PARRYA

Subsect. *Cembroides*

Of the eight species of nut pine, four are in the United States—*P. monophylla* Torr. & Fremont, *P. edulis* Engelm., and with *P. quadrifolia* Parl. and *P. cembroides* Zucc., ranging into Mexico. Four piñons are confined to Mexico, *P. culminicola* Andres. & Bearman, *P. maximartinezii* Rzed., *P. pinceana* Gord., and *P. nelsonii* (Shaw). Several varieties of *P. cembroides* have been recognized in recent years (Bailey, 1979, 1983 gives references). These appear to be geographic races of relatively recent, probably Quaternary, origin.

The *P. cembroides* population isolated in the mountains of the Cape Region, Baja California, named *P. cembroides* var. *lagunae* Robert-Passini (1981), poses an interesting problem. The Cape Region separated from the mainland of Jalisco by northward movement of the San Andreas and allied rifts and later spreading along the mid-ocean rise, which opened the Gulf of California. This raises the question as to whether *a*) there are relict stands of the Cape piñon in the Sierra Madre Occidental masquerading as *P. cembroides,* or whether *b*) the Cape population was on the mainland and became extinct here, or *c*) whether the pine originated in the Cape Region from a *cembroides* population that was isolated there as the Cape Region separated from the mainland.

Piñons do not intercross with other members of the genus (Mirov, 1967: 334), although pines of other subsections may do so. This implies that *Cembroides* are ancient, consistent with the fossil record, which shows that piñon was already present in the Middle Eocene (46 Ma).

Pinus ballii Brown, U.S. Geol. Surv. Prof. Paper 185: 53, pl. 8, fig. 5, 1934. TYPE: U.S.A. Colorado: Green River. U.C. Mus. Pal., holotype 1927–20688. Figures 10, 11.

Pinus ballii Brown. MacGinitie, Univ. Calif. Publ. Geol. Sci. 83: 91, pl. 25, fig. 2, 1969.

A 3-needled fascicle with deciduous sheath (Fig. 10) and an impression of a cone (Fig. 11) rep-

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FIGURES 8–18.—8. *Pinus florissantii* Lesquereux. Florissant, Colorado. Princeton Univ., holotype 144. Basal Oligocene, 34 Ma. (Previously figured by Lesquereux [1883] and MacGinitie [1953].)—9. *Pinus florissantii* Lesquereux. Creede, Colorado. U.C. Mus. Pal., hypotype. Late Oligocene, 26.5 Ma.—10. *Pinus ballii* Brown. Green River, Colorado. U.C. Mus. Pal., holotype 1927 (20688). Middle Eocene, 46–47 Ma. (From Brown, 1934.)—11. *Pinus ballii* Brown. Green River, Colorado. U.C. Mus. Pal., hypotype 20671. Middle Eocene, 46–47 Ma. (From MacGinitie, 1969.)—12. *Pinus sanjuanensis* Axelrod, sp. nov. Creede, Colorado. Univ. Colorado Mus., holotype 19701. Late Oligocene, 26.5 Ma.—13–16. *Pinus sanjuanensis* Axelrod, sp. nov. Creede, Colorado. U.C. Mus. Pal., paratypes 7239–7241, 7243. Late Oligocene, 26.5 Ma.—17. *Pinus lindgrenii* Knowlton. Chalk Hills, Idaho. Jurupa Cultural Center, California, hypotype 11205. Late Miocene, 5–6 Ma.—18. *Pinus lindgrenii* Knowlton. Chalk Hills, Idaho. U.S. Nat. Mus., holotype 8179. Late Miocene, 5–6 Ma. (From Knowlton, 1901.)

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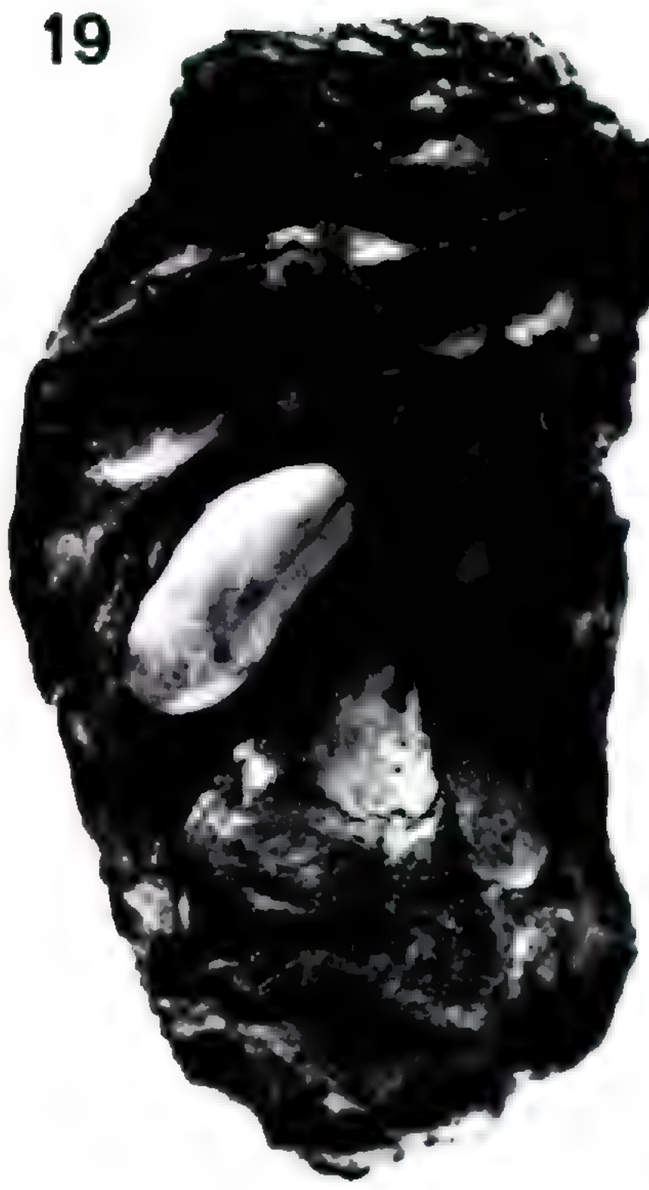

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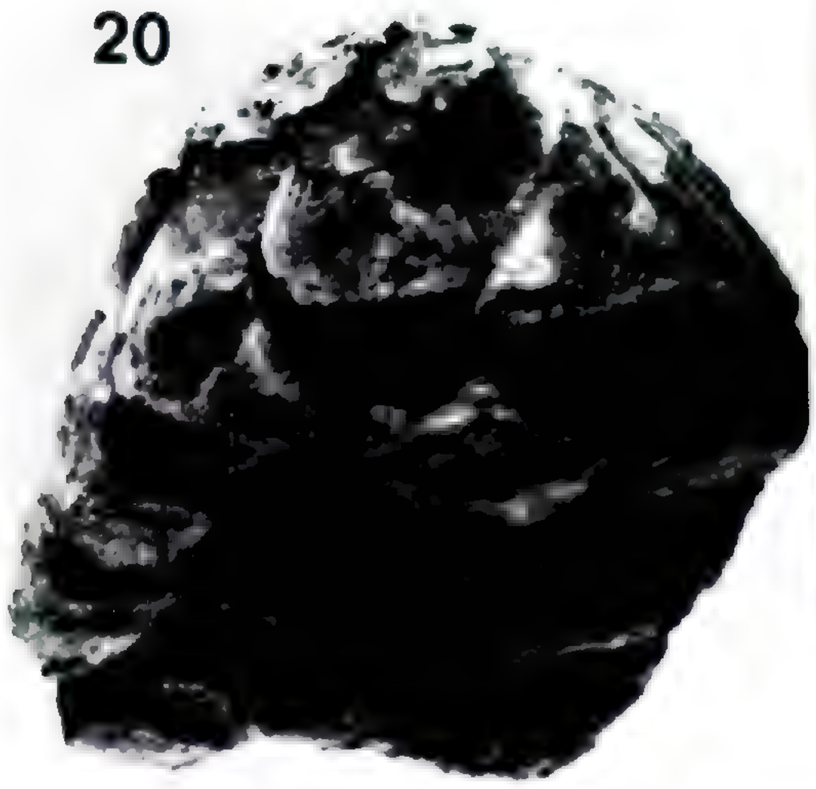

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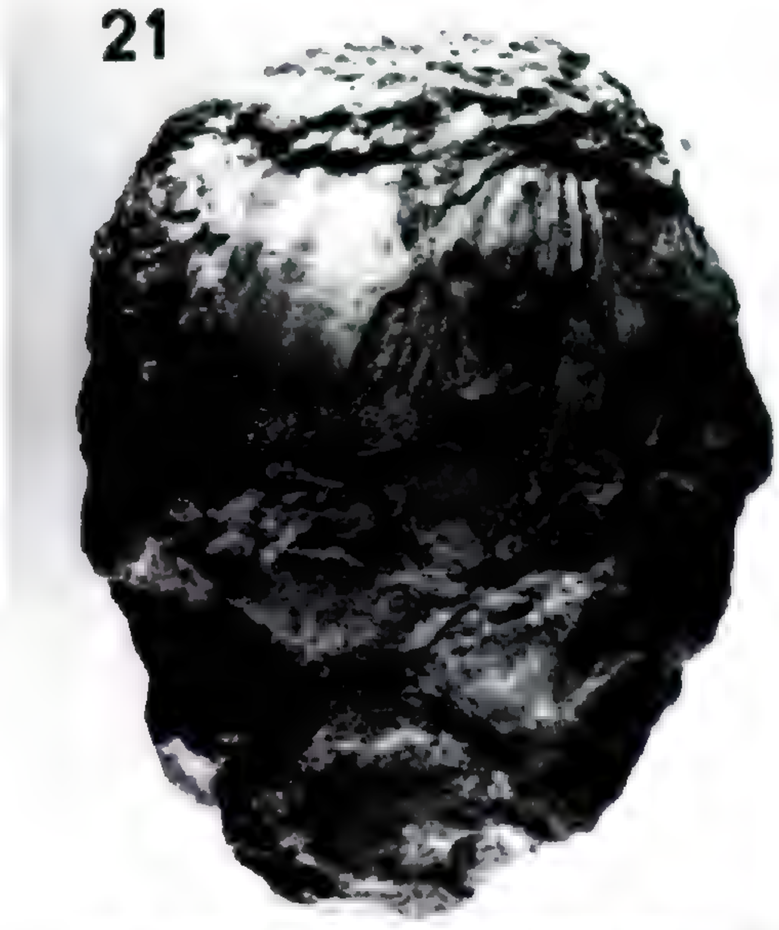

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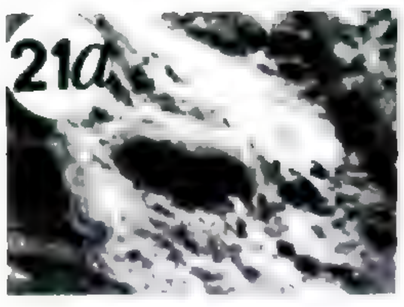

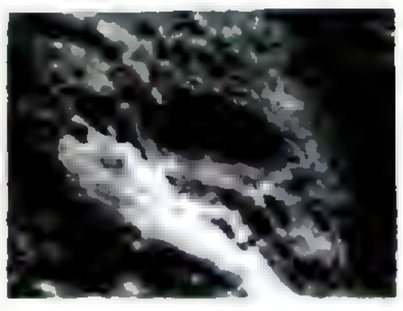

resent a piñon in the Middle Eocene Green River flora, dated at 46–47 Ma.

Occurrence. Green River, Colorado-Utah: U.C. Mus. Pal., hypotype 20671.

Pinus kelloggii Webber, Carnegie Inst. Wash. Publ. 412: 121, pl. 1, figs. 1–3, 1933. Ricardo, California. U.C. Mus. Pal., cotypes 156A–C.

Fossil wood from the lower part of the Ricardo Formation (12 Ma), Last Chance Gulch, on the south slope of the El Paso Mountains 40 km northeast of Mohave, California, has been identified as that of piñon. The associated flora includes woods of palm, oak, cypress, and locust.

Pinus kinnickensis Axelrod, sp. nov. TYPE: U.S.A. California: Tehachapi. U.C. Mus. Pal. holotype 1399. Figure 21*a*.

Pinus lindgrenii Knowlton. Axelrod, Carnegie Inst. Wash. Publ. 512: 85, 1939.

Seed ovoid in shape with an obtuse apex and rounded base, somewhat asymmetrically swollen, 1 cm long and 5 mm wide; testa very thin, and in one or two areas the papery nucellus still evident; endosperm with the contained embryo 7 mm long and 3 mm broad; oblong, rounded at one end and tapering at the other.

Discussion. During collecting of the Tehachapi flora, situated at the southeast end of the Sierra Nevada, a complete pine nut was uncovered in the andesite tuff that overlies the rhyolite tuff bed in which the fossil leaves occur. The specimen was identified as *P. lindgrenii* because at that time it was the only fossil piñon known and the pine nut seemed referable to it. Now that more numerous cones of *P. lindgrenii* are available (see below), it is evident that that species has much larger seeds than the Tehachapi specimen. It therefore represents a different species and is given a new name.

The complete specimen cannot now be illustrated because over the years the tuff in which it occurs has largely disintegrated, leaving only an impression of one side of the seed. Figure 21*a* shows the specimen in both concave and convex views.

Pinus lindgrenii Knowlton, Torreya 1: 113–115, text figs. 1–3, 1901. TYPE: U.S.A. Idaho: Chalk Hills. U.S. Nat. Mus. holotype 8179. Figures 17–21.

The silicified cone collected by one of Lindgren's associates, and described by Knowlton, comes from a site south of Bruneau, southern Idaho. It is from the Chalk Hills Formation (Malde & Powers, 1962) that has yielded diverse mammals that are judged to be Late Miocene (Hemphillian), or about 6–7 Ma. Other fossil plants in the formation include a bracket fungus and woods identified as fir, oak, alder, poplar, and hickory (Brown, 1940).

Additional cones collected by Ruth A. Kirkby add importantly to our understanding of the species and its position in the Subsect. *Cembroides*. Her collections come from the north end of Chalk Hills (sec. 19) and west of Highway 51 in sec. 25, T. 7 S, R. 4 E.

Supplementary description. Ovuliferous cones ovate to ovoid, base truncate, tip acute to obtuse; 5.0–7.0 cm long and 4.0–6.0 cm broad; cone scales thick, up to 2.5 cm broad in middle of cone, smaller elsewhere, the scales with low, broadly triangular apophyses; umbo centro-parvi-mucronate. Seeds wingless, very large, some in middle of cone 2.5 cm long, crudely tear-shaped, broader distally, larger than those of piñon today; shell of seed very thin.

Discussion. *Pinus lindgrenii* is generally allied to *P. cembroides* and *P. edulis* in that they also have low, triangular apophyses. However, their cones are smaller and the seeds are not so large as those of the fossils. *Pinus monophylla* and *P. quadrifolia* both differ from *P. lindgrenii* in that they have more prominent, raised apophyses, and also smaller cones and seeds. Cones of *P. pinceana* of the Sierra Madre Oriental are most similar to the fossil, though *P. lindgrenii* may represent a species intermediate between *P. pinceana* and a *P. cembroides-edulis* alliance.

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FIGURES 19–24.—19–21. *Pinus lindgrenii* Knowlton. Chalk Hills, Idaho. Jurupa Cultural Center, Riverside, California. Hypotypes 11200, 11201, 11204. Late Miocene, 5–6 Ma.—21*a*. *Pinus kinnickensis* Axelrod. Tehachapi, California. U.C. Mus. Pal., holotype 1399. Oriented to show concave and convex views.—22–24. *Pinus balfouroides* Axelrod. Thunder Mountain, Idaho. U.C. Mus. Pal., hypotypes 7186–7188. Middle Eocene, 45 m.y.

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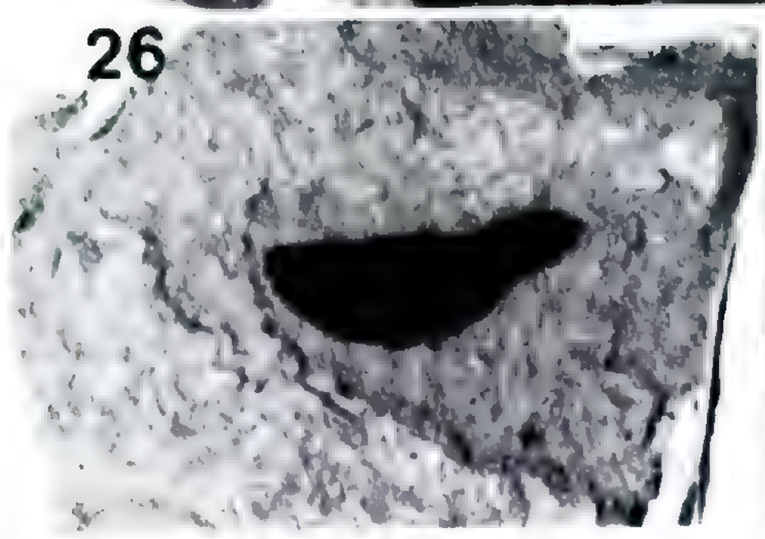

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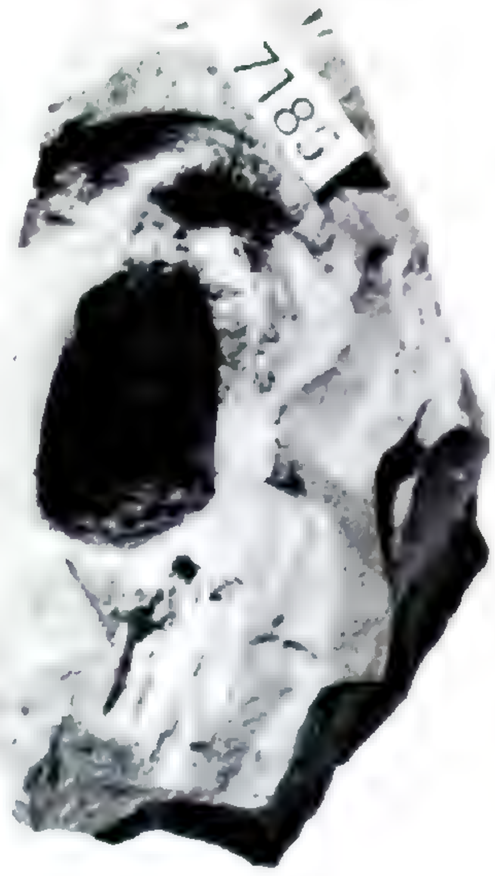

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The question may be raised as to whether the larger, more prominent, upswept apophyses of *P. monophylla* and *P. quadrifolia* reflect adaptation to a drier summer climate in the west. Some indication of this is seen in the western Arizona populations of *P. edulis* that have larger apophyses.

Occurrence. Chalk Hills, Idaho: Jurupa Mus. Nat. Hist., Riverside, California, hypotypes 11201, 11203–11205, homeotypes 11202–11206.

Pinus sanjuanensis Axelrod, sp. nov. TYPE: U.S.A. Colorado: Creede. U. Colo. Mus., holotype 19701; U.C. Mus. Pal., paratypes 7239–7244, 7247. Figures 12–16.

Imprint of near-proximal portion of globular cone; measures 4.0 by 4.5 cm in section; apophyses subdued; umbro mucronate, centro in position on scales; terminal ends of scales chiefly 5-sided and asymmetrically so; fascicles in 2s; 1.5–3.2 cm long, individual needles 1 mm wide, slightly curved; tips tapered to a sharply acute tip; base is a subdued, rounded remain of the deciduous sheath.

Discussion. The imprint of the cone cannot be separated from those of modern *P. edulis* cones. Needles in 2s occur at the Dry Creek localities, but were encountered only rarely at other sites. They are also comparable to those of the living *P. edulis* of the southern Rocky Mountains and northern Mexico. Many of its present associates have allied taxa in the Dry Creek florules, including species of *Cercocarpus, Fallugia, Holodiscus, Mahonia, Peraphyllum, Philadelphus, Quercus, Ribes, Robinia, Sapindus,* and others. The Dry Creek area has the best representation of vegetation of semiarid requirements in the Creede basin consistent with the occurrence of piñon there.

In her report on the Creede flora, Stewart (1940: 146) referred to fossil wood identified as a pine of the *Cembroides* alliance.

The only other pine in the Cordilleran region that seems related to this species is *P. ballii* Brown from the Green River flora, represented by a fascicle of three needles and a cone (MacGinitie, 1969). The 3-needled fascicle presumably is more nearly allied to *P. cembroides* which now ranges from southern Arizona into Mexico. The apophyses of the cone scales are more raised than those of *P. sanjuanensis.*

Subsect. *Balfourianae*

This small group includes *P. aristata* Engelm. of the central to southern Rocky Mountains, *P. longaeva* Bailey of the west-central Rocky Mountains and Great Basin ranges, and *P. balfouriana* Grev. & Balf., which is discontinuous from the Klamath Mountain area of northwestern California to the southern Sierra Nevada.

Pinus balfouroides Axelrod, Univ. Calif. Publ. Geol. Sci. 121: 209, 1980. TYPE: U.S.A. Nevada: Chalk Hills. U.C. Mus. Pal., holotype 8007, paratypes 8009–8013. Figures 22–33.

Pinus florissanti Lesquereux. Axelrod, Univ. Calif. Publ. Geol. Sci. 39: 227, pl. 42, fig. 9, 1962.
Pinus wheeleri Cockerell. Axelrod, ibid., p. 227, pl. 42, figs. 4–8, 1962.
Pinus quinifolia Smith. Axelrod, Ann. Missouri Bot. Gard. 63: 28, figs. 13–14, 1976.
Pinus sp. Brown, U.S. Geol. Surv. Prof. Paper 186-J: 167, pl. 45, fig. 9, 1937.

The above-listed material from the Purple Mountain (13 Ma) and Chalk Hills (12 Ma) floras, western Nevada (Axelrod, 1976, 1962), includes cones, winged seeds, and needles in 5s. They are similar to structures produced by *P. balfouriana* of high montane regions in California.

A new locality for the species is in the Middle Miocene Temblor Formation (15 Ma) at Sharktooth Hill, near Bakersfield, California (Fig. 29). In addition, numerous fascicles and a cone scale of the species are in the Coal Creek flora, Idaho (Fig. 30–33) dated at 29 Ma. Associated are species of *Abies, Larix, Picea, Pinus, Sequoiadendron, Chamaecyparis,* and diverse deciduous hardwoods, including *Acer, Betula, Carya, Cornus, Crataegus, Malus, Sassafras, Sorbus,* and *Zelkova.* Furthermore, impressions of cones and needles in 5s that represent *P. balfouroides* are in coarse, silicified sedimentary rocks at Dewey

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FIGURES 25–33.—25–27. *Pinus balfouroides* Axelrod. Purple Mountain, Nevada. U.C. Mus. Pal., hypotype 7177, 7178, 5501. Late Miocene, 13 Ma.—28. *Pinus balfouroides* Axelrod. Chalk Hills, Nevada. U.C. Mus. Pal., holotype 8007. Late Miocene, 12 Ma. (From Axelrod, 1962.)—29. *Pinus balfouroides* Axelrod. Sharktooth Hill, California. U.C. Mus. Pal., hypotype 7180. Middle Miocene, 15 Ma.—30–33. *Pinus balfouroides* Axelrod. Coal Creek, Idaho. U.C. Mus. Pal., hypotypes 7182–7185. Late Oligocene, 27 Ma.

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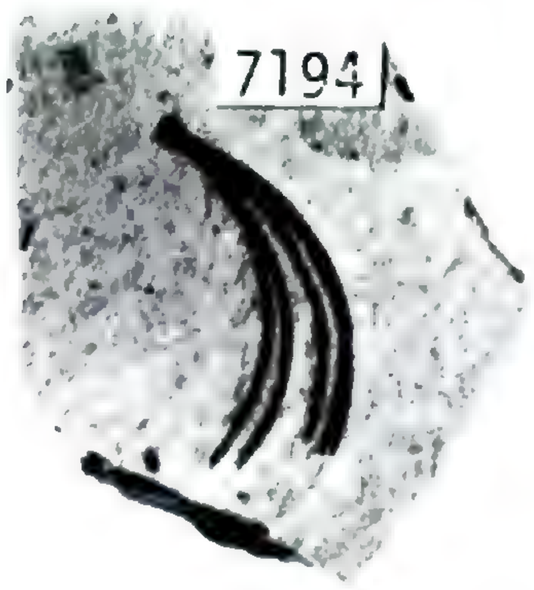

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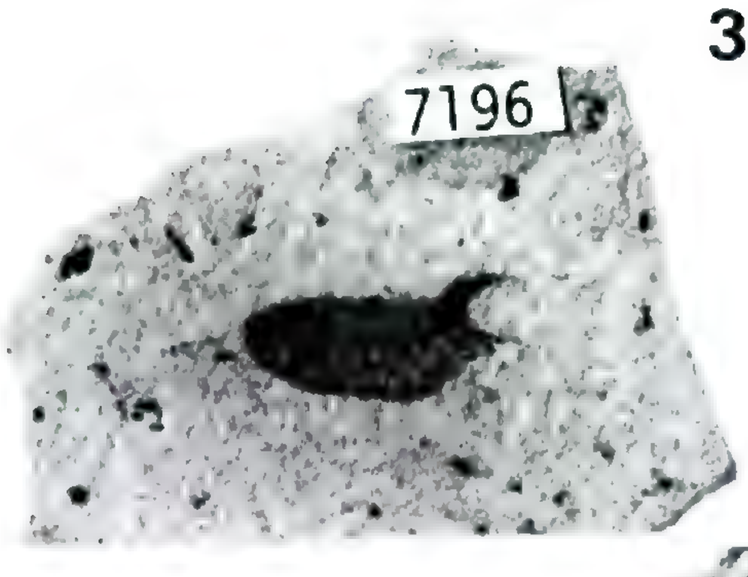

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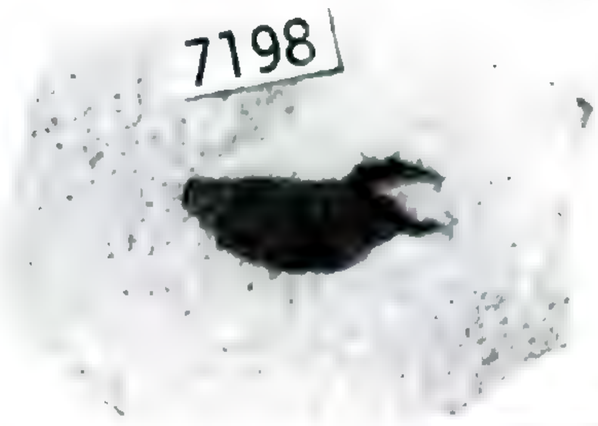

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Mine, Thunder Mountain, central Idaho (Figs. 22–24). Now at an altitude of 2,300 m, the fossils are in the Dewey Beds, a volcaniclastic subunit eroded from Sunnyside Rhyolite of the Challis Volcanics, and dated at ca. 46 Ma (Leonard & Marvin, 1984). The associated flora (Brown, 1937) is largely coniferous. It includes cones and foliage of *Abies, Larix, Picea, Pinus,* and *Sequoia,* as well as a few rare shrubby species of *Comptonia, Salix* and *Vaccinium.* The assemblage suggests a high montane environment, probably near 1,300 m.

Additional specimens from the Purple Mountain flora are also illustrated (Figs. 25–27). These occur with mixed conifer forest taxa, notably species of *Abies, Picea, Pinus, Chamaecyparis, Pseudotsuga,* and *Sequoiadendron* that lived near broadleaved sclerophyll vegetation composed of species of *Arbutus, Cercocarpus, Chrysolepis, Heteromeles,* and *Quercus.*

Occurrence. Purple Mountain, Nevada: U.C. Mus. Pal., hypotypes 5501–5502, 7177–7179; Sharktooth Hill, California: U.C. Mus. Pal., hypotype 7180; Coal Creek, Idaho: hypotypes 7182–7185; Thunder Mountain, Idaho: U.C. Mus. Pal., hypotypes 7186–7188; U.S. Nat. Mus. hypotype (unnumbered).

Pinus crossii Knowlton, U.S. Geol. Surv. Prof. Paper 131-G: 185, pl. 41, figs. 3, 8–10, 1923. Creede, Colorado. U.S. Nat. Mus., holotype 36514, paratypes 36511–36513. Figures 34–42.

Pinus crossii Knowlton. Axelrod, Univ. Calif. Publ. Geol. Sci. 59: 62, pl. 7, figs. 6–9, 1966. Bailey, Ann. Missouri Bot. Gard. 57: figs. 34–37, 1970.
Pinus aristata crossii Cockerell, Nature 133: 573, fig. 1, 1933.

Supplementary description. Cones long ovate, 8 to 10 cm long and 4.5 cm broad (closed in water); cone scales with long, sharp, upcurved prickles; needles in 5s, 1.1–3.0 cm long, with a conspicuous single groove present in the distal part; the needles on branchlets are crowded and bunched to give a fox-tail appearance; seed wings open, 1.2–2.0 cm long, the wing generally long oval, distal end rounded, 6–7 cm broad.

Discussion. The short, curved fascicles with needles in 5s that Knowlton named *Pinus crossii* are supplemented now by large suites of fascicles, branchlets with clusters of needles, winged seeds, and impressions of pine cones. All of this material is allied to *P. aristata* Engelm. of the southern Rocky Mountains in Colorado and northern New Mexico. However, there are sufficient differences to indicate that *P. crossii* probably is ancestral to the living bristlecone pine. The fossil cones are generally more robust and broader (as measured when closed in water) and also average larger, with most reaching 7.5 to 9.5 cm long and up to 4.5 cm broad. Furthermore, the fragile prickles, where well preserved, evidently were longer, for some are up to 8 mm long. Another difference is in the seed wing, which is broader and the seed, which is larger, than in most populations of *P. aristata* today.

The differences may be attributed to a more genial climate at the close of the Oligocene, with a longer growing season, more moisture, and milder temperature. It is noted that the abundant remains of *P. crossii* are associated with woodland taxa, notably species of *Chamaebatiaria, Cercocarpus, Fallugia, Juniperus, Peraphyllum, Mahonia,* and other members of that community. By contrast, *P. aristata* is confined now largely to drier, rocky sites at subalpine levels, reaching down on drier sites into the middle of the mixed conifer belt, well removed from piñon-juniper woodland vegetation today.

Occurrence. Creede, Colorado: U.C. Mus. Pal., hypotypes 7190–7198, homeotype 7246; U. Colo., hypotypes 18654, 19694, 19698, homeotype 19701; Copper Basin, Nevada: U.C. Mus. Pal., hypotypes 8873–8876, 8901, 8902; Titus Canyon Formation, Death Valley, California: U.C. Mus. Pal., hypotype 7189.

Subgenus Pinus

sect. ternatae

Subsect. *Leiophyllae*

Pinus coloradensis Knowlton, U.S. Geol. Surv. Prof. Paper 131-G: 186, pl. 41, fig. 6. 1923. TYPE: U.S.A. Colorado: Creede. U.S. Nat.

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FIGURES 34–42.—34–40. *Pinus crossii* Knowlton. Creede, Colorado. U.C. Mus. Pal., hypotypes 7190, 7191, 7193–7196, 7198. Late Oligocene, 26.5 Ma.—41, 42. *Pinus crossii* Knowlton. Titus Canyon, Death Valley, California. U.C. Mus. Pal., hypotype 7189. Figure 42 is a latex cast of Figure 41. Early Oligocene, ca. 37 Ma.

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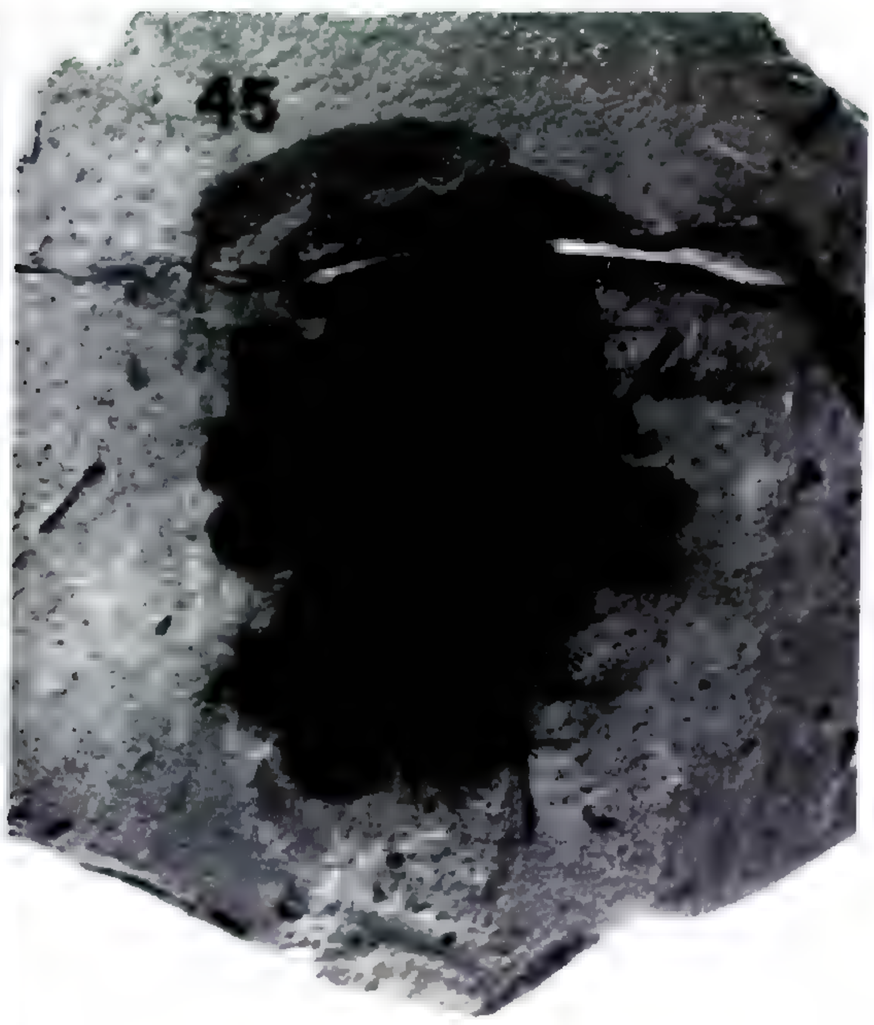
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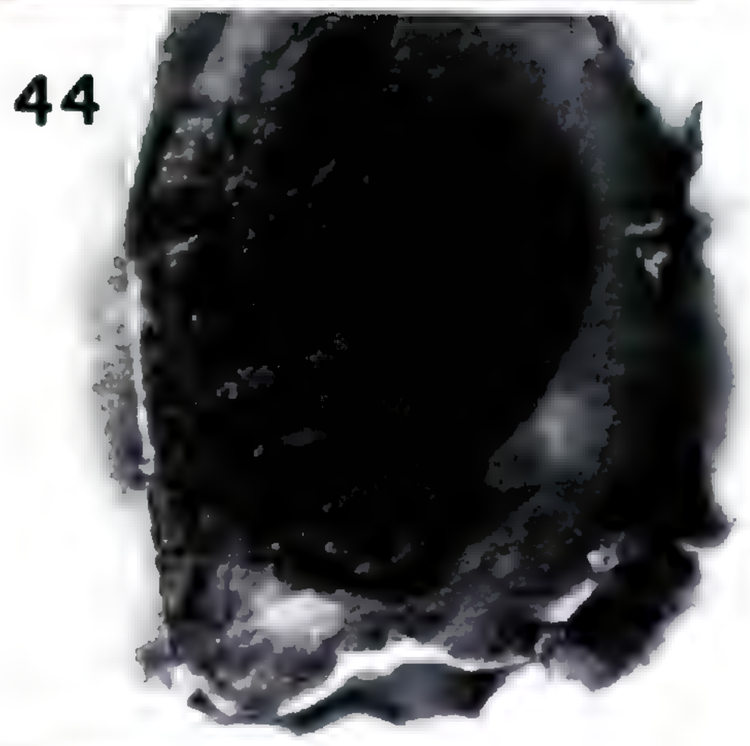
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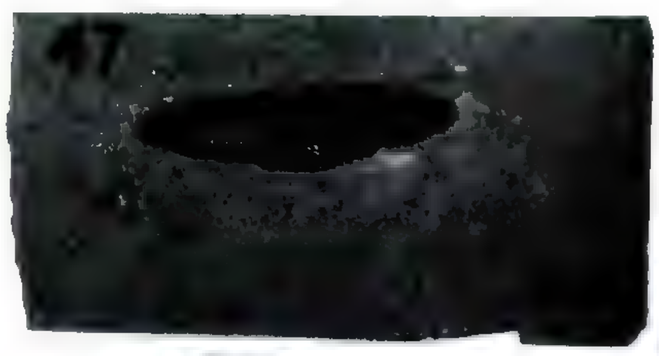
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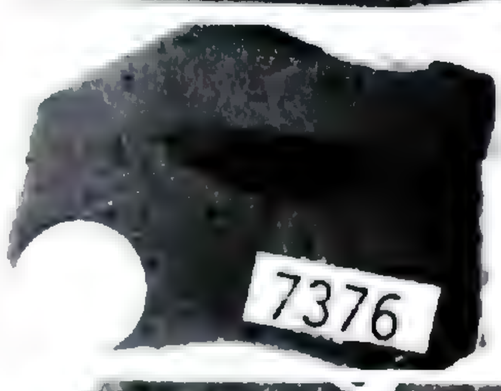
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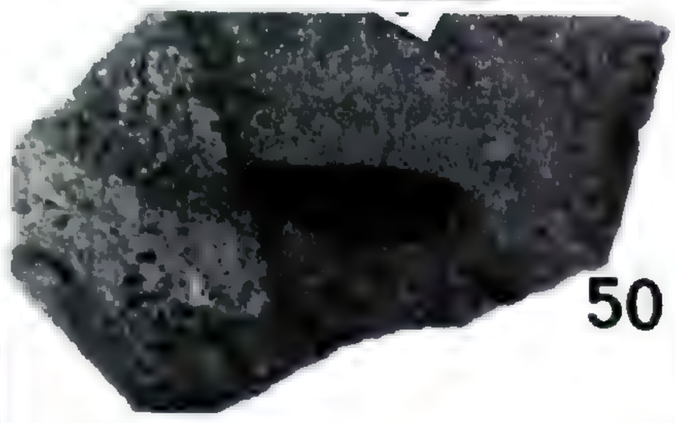
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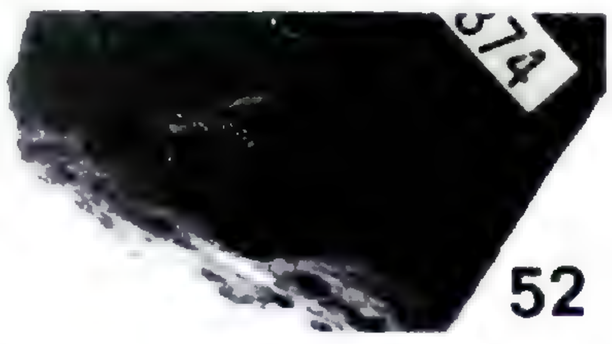
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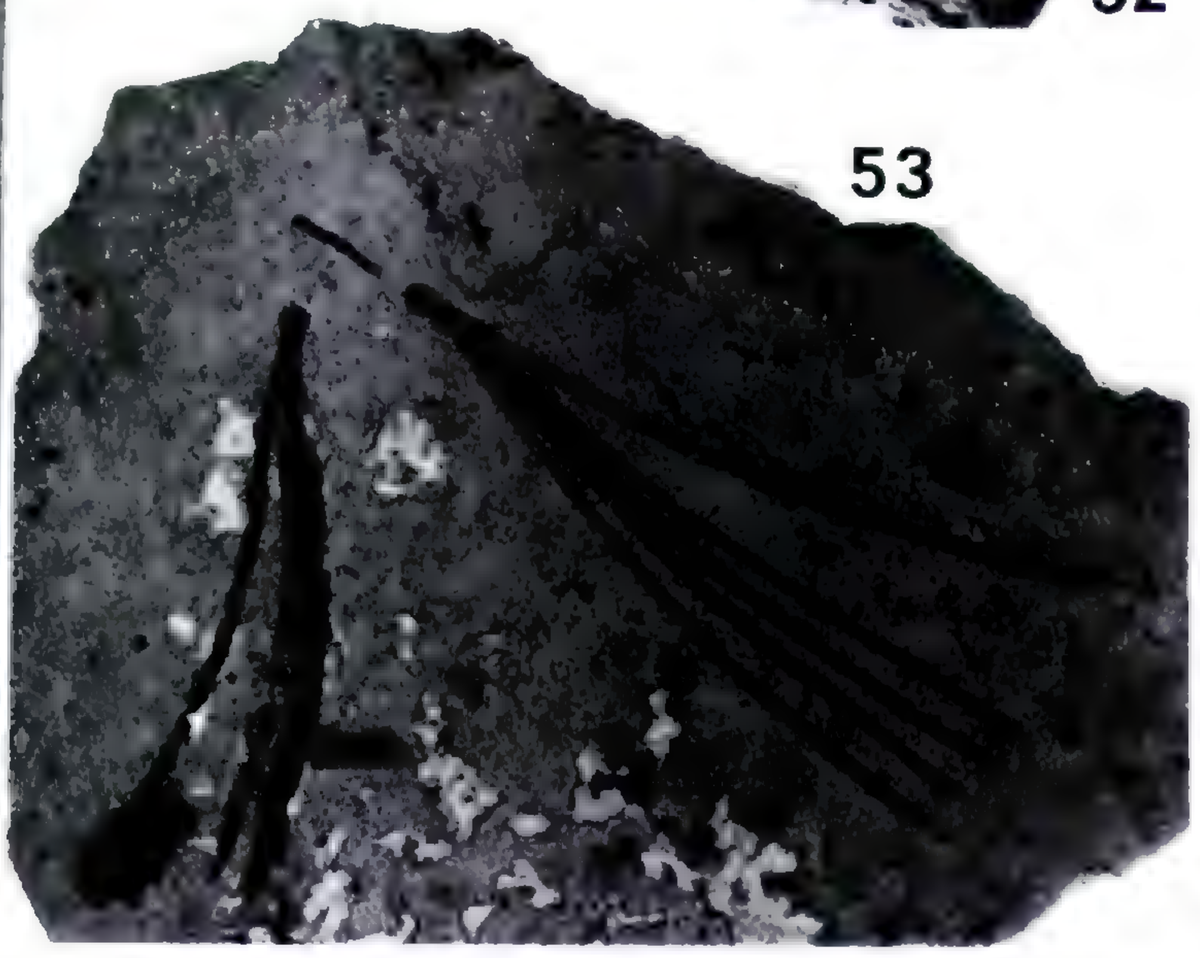
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Mus., holotype 36506. Figures 43–45, 47–53.

The type specimen was incorrectly illustrated. The cone scales are thin, not swollen as the retouched figure suggests. The following supplementary description is based on the type and an additional cone in the Univ. Colorado Museum, as well as foliage and winged seeds presumed to represent this species.

Supplementary description. Cones small, oval to elliptic in outline, truncate proximally, broadly obtuse distally, 3.0–4.5 cm long, 2.0–3.0 cm broad (open); cone scales thin, tips broadly rounded, slightly widened distally, and somewhat reflexed when open; umbo dorsal, centro erecto-mucronate. Needles in 5s, quite slender, 4–5 cm long, 0.5–1.0 mm broad, tapered distally to acute tip, base with small, rounded (deciduous) sheath. Winged seeds 2.0–2.1 cm long, seed wing narrow, 5–6 mm broad, elliptic, distal and rounded to blunt; seed 3–4 mm long, ovate, acute tip, rounded proximally.

Discussion. Knowlton (1923) suggested a general similarity between *P. coloradensis* and cones of *P. arizonica* Engelm. However, *P. arizonica* cones are larger, the cone scales are broader, and the cone is overall more massive. Closer relationship appears to be with *P. chihuahuana* Engelm. (= *P. leiophylla* var. *chihuahuana*), which ranges from southern Arizona to central Mexico, though needles of the fossil are somewhat shorter. Its occurrence at Creede is consistent with a number of Madrean taxa in the flora, including species of *Arbutus, Cercocarpus, Fallugia, Mahonia,* and *Populus* that range from Arizona well south into Chihuahua and Durango. *Pinus chihuahuana* is a common member of the middle and upper woodland belt, as well as the mixed-conifer forest zone, relations consistent with the nature of vegetation in the Creede flora.

Occurrence. U. Colo. Mus., hypotype 27381; U.C. Mus. Pal., hypotypes 7199–7202.

Pinus paucisquamosa Templeton, South. Calif. Acad. Sci. Bull. 52: 64–66, figs. 1, 2, 3b, 1953. TYPE: U.S.A. California: Altamira Shale, Nat. Hist. Mus. Los Angeles Co., holotype 1400. Figure 46.

This small, nearly complete cone is from the upper Altamira Shale at Point Fermin, San Pedro, California. It occurs in the *Bolivina modeloensis* foraminiferal subzone, of early Mohnian age, or about 14.5 Ma. (Woodring et al., 1946; Turner, 1970). It was initially compared by Templeton (1953) with *Pinus chihuahuana,* but Mirov (1967: 35) suggested that it may be a species of Sect. *Insignes,* described and illustrated by Shaw (1914). *Insignes* are now considered a heterogeneous group, comprising species of *Sylvestres* (*P. halepensis, P. pinaster*), *Australes* (*P. rigida, P. serotina, P. pungens*), *Contortae* (*P. virginiana, P. clausa, P. banksiana, P. contorta*), and *Oocarpae* (eight species, four of each in California and Mexico). Comparison with cones of these species reveals little evidence of relationship with *P. paucisquamosa.*

As suggested by Templeton, the fossil resembles the smaller cones of *P. chihuahuana* (= *P. leiophylla* Scheide & Deppe var. *chihuahuana*), which ranges from southern Arizona-adjacent New Mexico southward into central Mexico. However, in its broader cone scales the fossil shows greater relationship with cones of *P. lumholtzii* Robinson & Fernald, distributed from Sonora southward into Jalisco. *Pinus paucisquamosa* probably is an extinct member of the Leiophyllae.

This pine occurs in the marine Altamira Shale, which includes glaucophane schist debris similar to that in the Poway Formation. Both sites derived this debris from the landmass Catalinia, which then stood near the present shore (Reed, 1951: 170–171; Woodford et al., 1954: 71, 74; Woodring et al., 1946). Since the basement terrane west of the Inglewood-Newport fault, where the fossil occurs, differs significantly from that to the east, considerable displacement is implied. This most probably was from Mexico, because Miocene rocks similar to those of the Poway occur south of Ensenada and also on South Coronado Island (Stuart, 1974). The relationships

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FIGURES 43–53.—43. *Pinus coloradensis* Knowlton. Creede, Colorado. U.S. Nat. Mus., holotype 365061. Latest Oligocene, 26.5 Ma. (Previously figured by Knowlton, 1923.)—44. *Pinus coloradensis* Knowlton. A latex cast of specimen in Figure 43.—45. *Pinus coloradensis* Knowlton. Creede, Colorado. Univ. Colo. Mus., hypotype 27381. Latest Oligocene, 26.5 Ma.—46. *Pinus paucisquamosa* Templeton. Altamira Shale, California. Nat. History Mus. Los Angeles Co., cast of holotype A4432/PB-1400. Middle Miocene, 15 Ma.—47–53. *Pinus coloradensis* Knowlton. Creede, Colorado. U.C. Mus. Pal., hypotypes 7273, 7202, 7376, 7278, 7200, 7374, 7201. Latest Oligocene, 26.5 Ma.

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suggest that the Miocene fossil site was then opposite western Sonora where members of Subsect. *Leiophyllae* occur today, and probably did in the Middle Miocene (ca. 15 Ma).

SECT. PINUS

Subsect. *Sylvestres*

This alliance has 19 living species of which 11 are Asiatic, six European, and two American. The last include *P. resinosa* Aiton of the northeastern United States and adjacent Canada, and *P. tropicalis* Morelet of Cuba and Isle of Pines.

Several present European species reportedly have allied fossils in that region (see Mirov, 1967; Gaussen, 1960), but taxa of the alliance in North America are now known as fossil from only the Middle Eocene Allenby Formation (46 Ma) near Princeton, British Columbia (Stockey, 1984). Stockey analyzed the internal structure of cones and needles preserved in chert and showed that three taxa have the basic characters of *Sylvestres*. These include cones of *P. princetonensis* Stockey and *P. arnoldii* Miller and needles of *P. allisonii* Stockey. Whether these are to be grouped into a single species (*P. arnoldii* has priority) was left open by Stockey because the fossils are from different sites.

It is desirable to note that *P. clementsii* Chaney (1954) from the Late Cretaceous (85–86 Ma) of southern Minnesota was compared with *P. resinosa* Aiton. Examination of the mold that represents the type specimen (Chaney, 1954, figs. 1, 2) and a cast of it (Chaney, 1954, fig. 3) shows that the apophyses are raised and essentially convex. The structure of the umbo is largely erased, either by erosion or by weathering. Actually, there is insufficient detailed structure preserved to definitely relate the pine to a subsection. Furthermore, the paratype, which is from a locality some 25 miles distant, is only a small piece of a cone imprint. It certainly represents a different species as judged from the size and shape of the apophyses and the features of the umbo. It may represent a species of *Sylvestres* but is too incomplete for this to be certain. That either specimen is a pine can be disputed because their internal structure is indeterminate; both may be *Pityostrobus*.

From an ecological standpoint, the large dicotyledon leaves in the associated fossil flora indicate a warm temperate to subtropical climate (Chaney, 1954). If relationship with *Pinus resinosa* is accepted, it would be necessary to reconstruct high relief (1,000–1,500 m) in the region to provide a cold temperate climate for the pine. This would involve miles of transport via river, and, in view of the coarse grit and conglomerate in the section, the cones should be well worn, yet this is not the case. The evidence suggests that the *Pinus* (or *Pityostrobus*) species from southern Minnesota probably were members of the lowland flora, living on well-drained, drier south slopes not far from the areas of plant accumulation.

Occurrence. Minnesota, Cretaceous: Univ. Minnesota, Dept. Botany Paleobot. Coll., holotype no. C 770 (from Ochs Clay pit near Springfield), paratype no. C 711 (from near New Ulm, 25 miles east).

Subsect. *Australes*

This group of 11 species occurs in the southeastern United States, the Bahamas, Cuba, Hispanola, and Central America (Critchfield & Little, 1966, map 18). Fossil cones reportedly allied to *P. taeda* and *P. rigida* recorded from the Miocene of western Europe (in Gaussen, 1960) need to be reexamined before they can be accepted as valid records of Australes in Europe. One fossil species is now known for the group in the southeastern states.

Pinus collinsii Berry, Torreya 36: 124–127, text-fig. 2, 1936. TYPE: U.S.A. Maryland: Calvert Formation. U.S. Nat. Mus., holotype unnumbered and missing. Figures 57–59.

Pinus collinsii Berry. Berry, Wash. Acad. Sci. Jour. 31: 506–508, figs. 1, 2, 1941. St. Marys Formation, Maryland.

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FIGURES 54–59.—54. *Pityostrobus lynnii* (Berry) Miller. Aquia Formation, Belvedere Beach, Virginia. U.S. Nat. Mus., holotype 222786. Paleocene, ca. 60 Ma. (From Berry, 1934.)—55. *Pinus engelmannoides*, sp. nov. Axelrod. Creede, Colorado. U.C. Mus. Pal., holotype 7203. Late Oligocene, 26.5 Ma.—56. *Pinus macginitieii*, sp. nov. Axelrod. Creede, Colorado. Univ. Colo. Mus., holotype 19703. Late Oligocene, 26.5 Ma.—57. *Pinus collinsii* Berry. Calvert Formation, Stratford Cliffs, Virginia. U.S. Nat. Mus., hypotype. Middle Miocene, 15 Ma. (From Berry, 1941.)—58. *Pinus collinsii* Berry. Calvert Formation, near Plum Point, Maryland. U.S. Nat. Mus., hypotype. Middle Miocene, 15 Ma. (From Berry, 1941.)—59. *Pinus collinsii* Berry. Calvert Formation, near Plum Point, Maryland. U.S. Nat. Mus., holotype. Middle Miocene, 15 Ma. (From Berry, 1936.)

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Cones recovered from the Middle Miocene Calvert and St. Marys Formations, Maryland, are similar to those of the living *Pinus taeda*, a widely-distributed species along the Atlantic and Gulf coastal plain from Delaware into eastern Texas. Associates of *P. collinsi* in the Calvert flora (Berry, 1916) include *Berchemia, Cassia, Nyssa, Platanus, Quercus, Salix,* and *Ulmus* that occur with *P. taeda* today.

Occurrence. St. Marys Formation, Maryland. U.S. Nat. Mus., specimen missing from collection and unnumbered.

Pityostrobus lynnii (Berry) Miller, Torrey Bot. Club Bull. 104: 5–9, figs. 1–7, 1977. *Pinus lynnii* Berry, Wash. Acad. Sci. Jour. 24: 182–183, fig. 1, 1934. TYPE: U.S.A. Virginia: Aquia Formation. U.S. Nat. Mus., holotype 22786.

The well-preserved cone described by Berry (1934), from the Aquia Formation, is now considered Paleocene in age (in Miller, 1977b). It has the external features of a species of *Australes* and resembles cones of *P. taeda* as well as those of *P. elliottii* Engelm. and *P. caribaea* Morelet, although the last two are on average larger than the fossil.

The internal structure of an additional cone studied by Miller (1977b) shows that it represents the extinct genus *Pityostrobus*. The bract-trace is free, and the scale has a thin, not a thick, vascular strand. Apart from these differences, in its general structure and shape it certainly seems to foreshadow pines of Subsect. *Australes* and may well have given rise to a species that produced cones similar to those of *P. taeda*.

Occurrence. Aquia Formation, Virginia: U.S. Nat. Mus., hypotype 201950.

Subsect. *Ponderosae*

This large group of living pines includes 13 species, most of which are in Mexico. A few fossil cones are known that resemble those of different species of the alliance. Identification of fossil winged seeds and fascicles poses a major problem, because those of many modern species are so similar that their reference to any one fossil species seems doubtful. In spite of the uncertainty, there are numerous records of large seed wings (without seeds) that appear to represent those similar to the western *P. ponderosa* Lawson. These have been recorded at several localities in the Rocky Mountains, including the Green River (46 Ma), Florissant (34 Ma), Ruby and Beaverhead (ca. 30 Ma), and Creede (26.5 Ma) floras. In the Great Basin, there are similar records in the Fallon (12 Ma), Middlegate (18 Ma) and Fingerrock (16 Ma) floras.

The following are records of fossil cones that appear to represent members of this subsection.

Pinus engelmannoides Axelrod, sp. nov. TYPE: U.S.A. Colorado: Creede. U.C. Mus. Pal., holotype 7203a, b. Figure 55.

Cone closed (in water), narrowly elliptic; 11–12 cm long, 4.5 cm broad proximally; broadly rounded or blunt proximally, apex acute; scales with prominent apophyses, asymmetrically triangular and upcurved; umbo apparently centro-reflexo-mucronate.

Discussion. This cone from the Creede flora resembles those produced by *P. engelmannii* Carr. in the Santa Rita and Chiricahua mountains, southeastern Arizona. It descends from the mixed-conifer forest zone to mingle with the middle to upper part of the oak woodland belt, an association similar to the vegetation setting at Creede. Among its associates at altitudes near 1,830 m (6,000 ft.) are *Pinus leiophylla, P. ponderosa, Pseudotsuga glauca, Juniperus deppeana, Arbutus arizona, Cercocarpus breviflorus,* and numerous oaks. From southern Arizona, *Pinus engelmannii* ranges southward in the Sierra Madre Occidental to Zacatecas, central Mexico.

Pinus macginitieii Axelrod, sp. nov. MacGinitie, Carnegie Inst. Wash. Publ. 599: 84, pl. 20, figs. 1, 3, 4, 1959. TYPE: U.S.A. Colorado: Florissant. U.C. Mus. Pal., lectotype 3776, paratype 3778; U.S. Nat. Mus., paratype 33758. Figures 56, 60–62.

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FIGURES 60–67.—60. *Pinus macginitieii* Axelrod, sp. nov. Florissant, Colorado. U.C. Mus. Pal., lectotype 3776.—61, 62. *Pinus macginitieii* Axelrod, sp. nov. Florissant, Colorado. U.C. Mus. Pal., paratype 3778, U.S. Nat. Mus., paratype 33758.—63–67. *Pinus ponderosoides* Axelrod, sp. nov. Creede, Colorado. U.C. Mus. Pal., holotype 7204, paratypes 7204–7208; Fallon Nevada, U.C. Mus. Pal., hypotypes 2034, 2035; Nevada, Aldrich Sta., U.C. Mus. Pal., hypotypes 4000, 4001.

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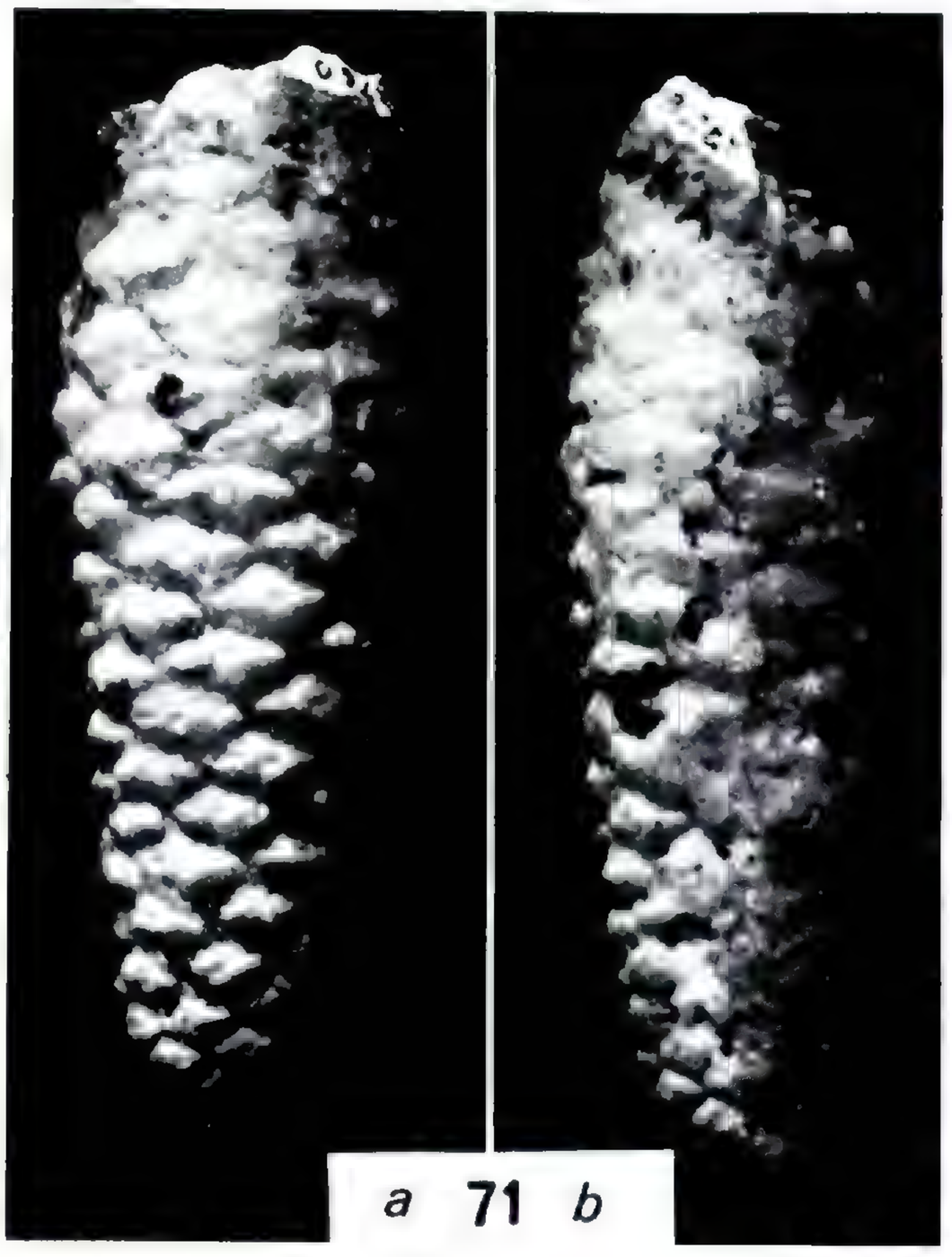

a 71 b

Pinus florissanti Lesquereux. Becker, Palaeontographica 127-B: 61, pl. 6, figs. 3, 5, 6, 9 (not figs. 1–2, 4, 7–8, 10, which may be a different species), 1969.

The Florissant pine represented by long needles in 3s with a long persistent sheath, together with large seed wings is clearly of the *Ponderosae* alliance. Similar seeds in the Beaverhead flora (Becker, 1969) evidently represent the same species as does a single large seed wing in the Creede flora.

Needles in 3s, 17.5 cm or more long, with a large persistent sheath, needles grooved, 1–2 mm broad, tips acute; seed wings 2.5–3.7 cm long, 0.8–1.0 cm broad, tips rounded to asymmetrically acute; large seeds, ovate, 8–9 mm long and 4–7 mm broad.

Discussion. The above listed fossils do not represent *P. florissanti* because the type specimen is a cone similar to those of *P. flexilis.* It has needles in 5s, and the seed wings are attached to the scales. *Pinus macginitieii* is allied to species of Subsect. *Ponderosae,* but not to *P. ponderosa,* which has smaller winged seeds. Closer comparison may be made with *P. michoacana* Martinez, a species now in Mexico from Jalisco southward into Chiapas. The relation of the seeds to the large cones of *P. riogrande* in the Creede flora, which is compared with the living *P. montezumae* Lamb., is uncertain; they may be allied.

This species is named for Dr. Harry D. MacGinitie whose monographs on western Tertiary floras stand as excellent contributions to Tertiary paleobotany.

Occurrence. Beaverhead, Montana: N.Y. Bot. Gard., hypotypes 146a–b, 147, 144, 916; Creede, Colorado: Univ. Colorado Mus., hypotype 19703.

Pinus ponderosoides Axelrod, sp. nov. TYPE: U.S.A. Colorado: Creede. U.C. Mus. Pal., holotype 7204, paratypes 7206–7208. Figures 63–67.

Pinus florissantii Axelrod, Univ. Calif. Publ. Geol. Sci. 33: 276, pl. 4, figs. 19–20; pl. 17, figs. 10–11, 1956.

Cone fragment 7 cm long, scales 1.3–1.4 cm broad, 7–8 mm high, umbo centro mucronate, prickle upturned, sharp. Needles 8 cm or more long, fascicles in 3s with large persistent sheath, needles grooved, 1–2 mm broad, tips acute; seed wings 2.0–1.5 cm long, wing 6 mm broad, long elliptic, tip broadly rounded to bluntly acute; seed ovate, 4–5 mm long, 3–4 mm broad, dehiscent.

Discussion. The specimens of *P. macginitieii* in the Florissant flora cited above demonstrate that Subsect. *Ponderosae* was already in existence in the Eo-Oligocene transition. An older record of Subsect. *Ponderosae* is that of *P. premurrayana* Knowlton from the Absaroka Volcanics, of Middle Eocene age as noted below. Specimens in the Creede flora referred to *P. ponderosoides* seem more similar to structures produced by the *P. scopulorum* of the Rocky Mountains.

The relation of this species to other fossils—chiefly winged seeds—that have been compared with *P. ponderosa* is uncertain because most of them are difficult (or impossible) to separate from other members of the *Ponderosae.*

Occurrence. Fallon, Nevada: U.C. Mus. Pal., hypotypes 2034, 2035; Aldrich Station, Nevada: U.C. Mus. Pal., hypotypes 4000, 4001.

Pinus premurrayana Knowlton, U.S. Geol. Surv. Monogr. 32, pt. 2: 677, pl. 82, fig. 5, 1899. TYPE: U.S.A. Wyoming: Langford Formation. U.S. Nat. Mus., holotype 222760. Figure 71*a–b.*

This silicified cast of a cone recovered from the east side of Yellowstone Lake was compared by Knowlton with *P. murrayana.* It shows no relationship to cones of that species, either in size, shape, or the nature of the cone scales. The cone, refigured here in two views, appears to be a member of Subsect. *Ponderosae.* It resembles the slender cones of *P. lindleyii* Loudon (see Shaw, 1914, pl. 25, fig. 223), considered by some to be a variety of *P. montezumae* Lamb. It is also assigned to *Ponderosae* because woods representing two species of fossil pine from the Yellowstone fossil forest have characters that place them in the hard-pine group (Read, 1930), of which the *Ponderosae* are a part. In addition, needles of *P. iddingsii* Knowlton from the Yellowstone

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FIGURES 68–71.—68. *Pinus riogrande* Axelrod, sp. nov. Creede, Colorado. U. Colo. Mus., holotype 19704. Late Oligocene, 26.5 Ma.—69, 70. *Pinus riogrande* Axelrod, sp. nov. Creede, Colorado. U. Colo. Mus., paratypes 7209, 7210. Late Oligocene, 26.5 Ma.—71*a, b. Pinus premurrayana* Knowlton. Langford Formation, East of Yellowstone Lake, Wyoming. U.S. Nat. Mus., holotype 222,760. Two views of specimen. Early Middle Eocene, 50 Ma.

flora (Knowlton, 1899: 680, pl. 82, figs. 8, 9) are in 3s, are 13+ cm long, are rounded and flat on one side and channeled on the other. They are much like needles of *Ponderosae* today.

The precise site at which *P. premurrayana* was collected is unknown. However, discussion with J. Richmond of the U.S. Geological Survey and R. Baker, University of Iowa, both of whom have been actively engaged in the geology of the area, indicates that the fossil cone is from the Absaroka Volcanics. These contain much silicified wood on the east side of the Yellowstone Lake, whereas the Pleistocene (Sangamon) sedimentary rocks there have plant remains but they are not silicified. The volcanic rocks on the east side of the Yellowstone Lake represent the Langford Formation of the Absaroka Volcanic Supergroup, and are K/Ar dated at 50 Ma, or early Middle Eocene (*in* Smedes & Protska, 1972).

Pinus riogrande Axelrod, sp. nov. TYPE: U.S.A. Colorado: Creede. Univ. Colo. Mus., holotype 19704; U.C. Mus. Pal., paratypes 7209–7211. Figures 68–70.

Cones large, long elliptic to elliptic-ovate; complete specimen 12.3 cm long, 4.5 cm broad in middle; largest broken cone over 15 cm long and 6 cm broad; bluntly rounded apex and base; 9 × 11 rows of cone scales, the middle ones 1.5 cm broad, 1 cm high; umbo dorsal, centro-reflexed, short mucronate, prickles 2–3 mm long, directed distally.

Discussion. These large cones resemble those of the living *P. montezumae* Lambert, distributed now from Durango and Nuevo Leon southward into Guatemala. The modern species varies in cone and needle size with increasing altitude. As documented by Shaw (1914) and Martinez (1948), these structures decrease in size with altitude and have been described as a series of varieties. The fossils resemble cones from localities at moderate elevations, consistent with the ecology indicated by the Creede flora in which they occur.

Pinus truckeensis Axelrod, sp. nov. U.S.A. Nevada: Celetom Quarry. U.C. Mus. Pal., holotype 7223, paratype 7224. Figures 72*p, a* & 73.

Cone broadly elliptic in outline; base truncate, apex obtuse; 15 by 11 cm, with proximal end deciduous on branch, so cone probably up to 17 or 18 cm long; 12 × 14 rows of cone scales; those in middle of cone on symmetrical (posterior) side are 1.7–2.5 cm broad, on asymmetrical (anterior) side (1 cone only) 2 cm broad; apophyses broadly rhombohedral, symmetrical on one side (Fig. 72*p*), asymmetrical on the other and upswept (Fig. 72*a*); centro-mucronate and erect or reflexed; prickle not preserved.

Discussion. Two specimens are in the collection. The strongly asymmetrical cone was preserved as a mold diatomite. By gradually filling the cavity with latex, a cast of the entire cone was removed to display both sides (Fig. 72*p, a*). The other cone (Fig. 73) shows the complete face on the symmetrical (posterior) side. On its lower margin, evidence of asymmetry of the anterior side is evident. Both specimens are referred to one species.

The fossils resemble cones produced by *P. pseudostrobus* Lindl. The chief difference is that the fossil cones are somewhat larger than those in the collection available for comparison at the Institute of Forest Genetics, Placerville. In addition, the apophyses are proportionately larger. Otherwise, there appear to be no significant differences between these species. *Pinus pseudostrobus* ranges from the mountains of central Mexico to Chiapas and Guatemala, inhabiting the conifer forest and the oak-madrone woodland at altitudes from 2,300 to 3,200 m.

The occurrence of a pine of southern affinity in western Nevada is not unique for the area. Other taxa in the Miocene record there that have their nearest allies in the Southwest, or in adjacent Mexico, include species of *Arbutus, Bumelia, Cercocarpus, Fraxinus, Mahonia, Populus, Quercus,* and *Sapindus,* and they are more numerous in the Miocene of southeastern California.

The fossil cones occur in diatomite of the Coal Valley Formation, exposed at the Celetom Quarry of the Eagle-Picher Industries, 30 km east of Reno. The deposit is about 12.5 Ma old as judged from radiometric dates of closely associated rocks nearby.

Subsect. *Sabinianae*

There is only a very limited record of this group of large-coned pines represented now by three living species. *Pinus sabiniana* Doug. inhabits the foothills of the inner Coast Ranges of central and northern California and the lower west slopes

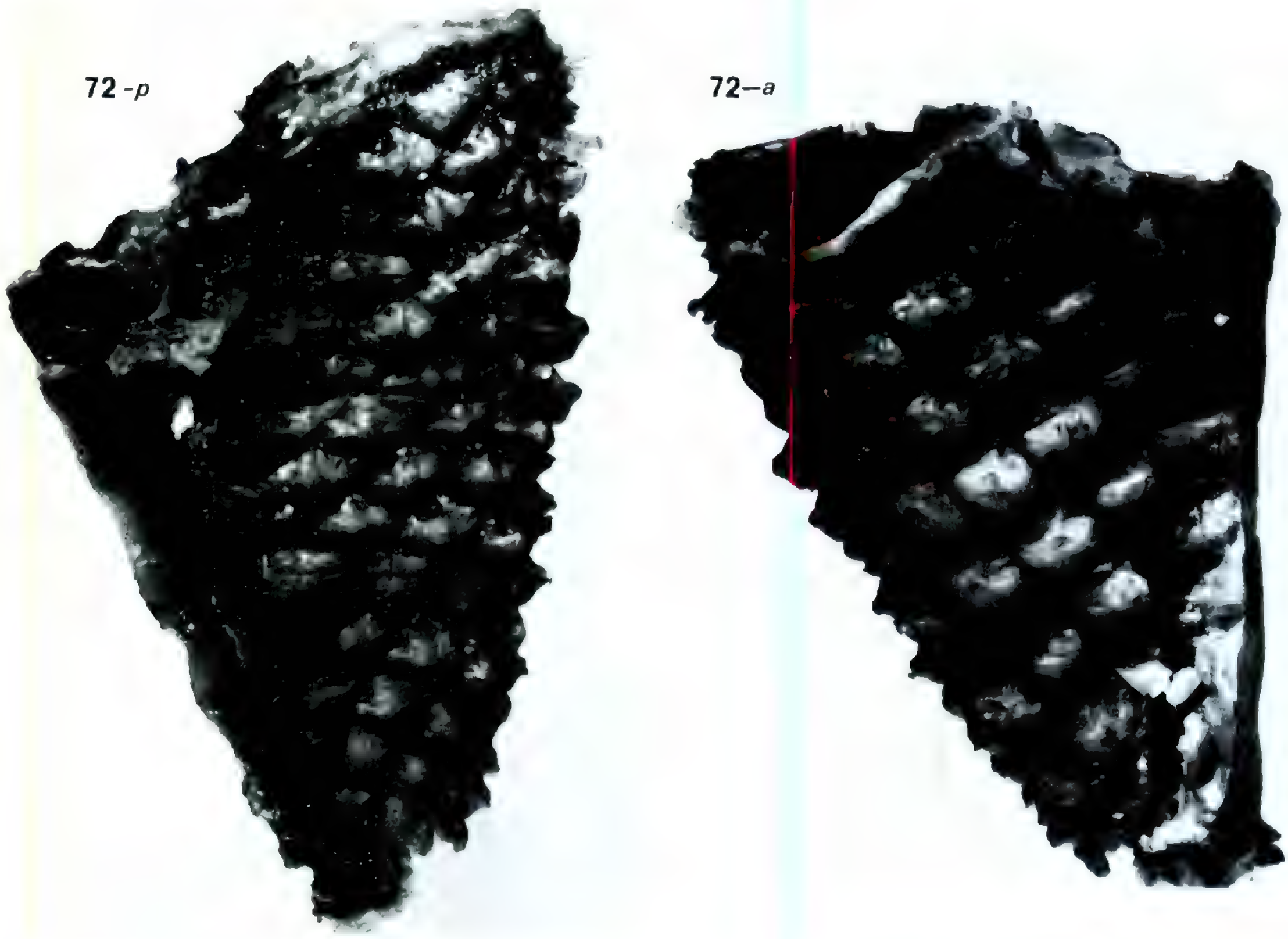

FIGURE 72. *Pinus truckeensis* Axelrod, sp. nov. Celetom Quarry, 30 km E. of Reno, Nevada. U.C. Mus. Pal., holotype 7223. Two views of specimen: *p, left* or posterior side; *a, right* or anterior side. Late Miocene, 12 Ma.

of the Sierra Nevada. *Pinus coulteri* D. Don occurs chiefly in the mountains of southern California at medium altitudes, ranging discontinuously northward in the Coast Ranges to Mount Diablo east of San Francisco Bay. *Pinus torreyana* Parry is a narrow endemic on the coast near La Jolla, and a subspecies occurs on Santa Rosa Island west of Santa Barbara (Haller, 1986).

The origin of the group is obscure but may lie with *P. oaxacana* Mirov of Mexico (Haller, 1966). It has similar cones as well as long needles in 5s. From this standpoint, there was an increase in cone size (*P. sabiniana, P. coulteri*) and the development of more armed cones with hooked apophyses. *Pinus oaxacana* occurs now in the Sierra Madre Occidental from Durango southward into Nayrit. In the early Neogene, forerunners of *P. torreyana,* as well as *P. sabiniana* and *P. coulteri,* may have separated from an ancestral *oaxacana*-like group and were then transported northward as the San Andreas fault system was activated (Crowell, 1979).

Mason (1927) identified specimens from the Bridge Creek and Cove Creek floras, Oregon, as *P. torreyana* Parry. However, these 5-needled fascicles with long, persistent sheaths are also similar to those of several *Ponderosae* taxa now in Mexico, as well as others (see Martinez, 1948).

Pinus hazenii Axelrod, Carnegie Inst. Wash. Publ. 476: 165, pl. 2, fig. 4, 1937. TYPE: U.S.A. California: Mount Eden. U.C. Mus. Pal., holotype 958, paratypes 7225, 7226. Figures 75, 76.

Very large cone scales, with large, hooked apophyses sharply constricted above suggest that this pine may be allied to *P. coulteri.* Additional material is needed to ascertain more definitively its relationship to that species.

P. coulteri produces one of the largest, most massive cones of living (and probably fossil) pines.

Pinus pieperi Dorf, Carnegie Inst. Wash. Publ. 412: 69, pl. 5, figs. 7–10, 1930. TYPE: U.S.A.

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cm
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California: Pico Formation. U.C. Mus. Pal., holotype 305, paratype 304. Figure 74.

Pinus pieperi Dorf. Axelrod, Carnegie Inst. Wash. Publ. 476: 165, pl. 2, figs. 2, 3, 1937. Axelrod, Carnegie Inst. Wash. Publ. 590: 144, pl. 2, fig. 1, 1950. Axelrod & DeMéré, San Diego Mus. Nat. Hist. Trans. 20: 292, fig. E, 1984.

The above records of fossil digger pine are from the Pliocene and Late Miocene of southern California. *Pinus sabiniana* does not occur in that area today except at its northern margin in Santa Ynez Valley north of Santa Barbara and at the north end of Liebre Mountain, southeast of Tejon Pass. The species is recorded also in the Pleistocene of southern California at Seacliff (Axelrod, 1983), Carpinteria (Chaney & Mason, 1933), and Lake Canyon east of Ventura (Wiggins, 1951).

This species may have disappeared from southern California during the post-glacial Xerothermic period, which brought interior and semidesert species to the coastal strip (Axelrod, 1966: 42–55).

Occurrence. Anaverde Formation, California: U.C. Mus. Pal., hypotype 3269; Mt. Eden Formation, California: U.C. Mus. Pal, hypotypes 959, 960, 7227; Diego Formation, California: San Diego Mus. Nat. Hist., hypotype 25168.

Subsect. *Contortae*

This alliance includes four living species. Two are in the eastern United States, *P. clausa* (Chap.) Vasey of Florida and southern Alabama, and *Pinus virginiana* Miller of the Appalachian province. *Pinus banksiana* Lamb. ranges from the Lake States northward across Canada to the MacKenzie River and east to Nova Scotia. *Pinus contorta* Dougl. (with three vars.) occupies the Rocky Mountains north of southern Colorado (var. *latifolia*), extends down the Cascade-Sierra Nevada axis into northern Baja California (var. *murrayana*), and has an outer Coast Range occurrence from coastal northern California into Alaska (var. *contorta*).

Pinus alvordensis Axelrod, Carnegie Inst. Wash. Publ. 553: 251, pl. 42, fig. 4, 1944. TYPE: U.S.A. Oregon: Alvord Creek. U.C. Mus. Pal., holotype 2095. Figures 77–84.

Supplementary description. Cone ovate, markedly asymmetrical and reflexed, rounded proximally, with a blunt apex; 3 cm long and 2 cm broad; peduncle short and thick, about 4 mm broad, 3 mm long (broken); 6 rows of cone scales, with sharply triangular, attenuated apophyses, slightly curved. Needles in 2s, 2.7–3.0 cm long, 1 mm broad, acute tips, base with a rounded sheath, 2–3 mm long, 2.0–2.5 mm broad. Winged seeds 1.5–2.0 cm long, 0.4–0.6 mm broad, wings slender, markedly acute distally; seed ovate, 5–6 mm long, acute distally.

Discussion. The cone from the Bull Run flora, northern Nevada, falls readily within the Subsect. *Contortae.* The relatively small size of the cone suggests that it may represent an early member of the group, although in the light of only a single specimen this cannot be demonstrated. The age of the deposit at this site (Loc. P 572–5) is 38 Ma, or Late Eocene. The associated flora represents a pure montane conifer forest of *Abies* (3 spp.), *Picea* (3 spp.), *Pinus* (2 spp.), *Larix, Tsuga,* and *Chamaecyparis* as dominants, with rare small leaves of forest shrubs, notably species of *Crataegus, Mahonia, Prunus,* and *Vaccinium.*

Slender winged seeds in the Creede flora, Colorado, are sufficiently similar to the Alvord Creek specimen to be referred to it. The Creede specimens are from 1.5 to 2.0 cm long, wings narrowly elongate, acute to rounded distally, wing 4–5 mm broad, seed proper about one fourth size of wing; tip acute; seed permanently attached to wing.

The needles in 2s are broadly similar to those of *P. sanjuanensis* Axelrod from the Creede flora. The latter can be distinguished because the fascicle sheath is smaller as compared with those of *P. alvordensis.*

There is no clear evidence that fossils from these sites are allied to any one of the modern varieties of *P. contorta,* although this may be modified as larger collections become available.

Occurrence. Creede, Colorado: U. Colo. Mus., hypotypes 19706, 19707; hypotype 19709; U.C. Mus. Pal., hypotypes 7174–7175, 7237,

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FIGURE 73. *Pinus truckeensis* Axelrod, sp. nov. Celetom Quarry, 30 km E. of Reno, Nevada. U.C. Mus. Pal., paratype 2224. Late Miocene, 13 Ma.

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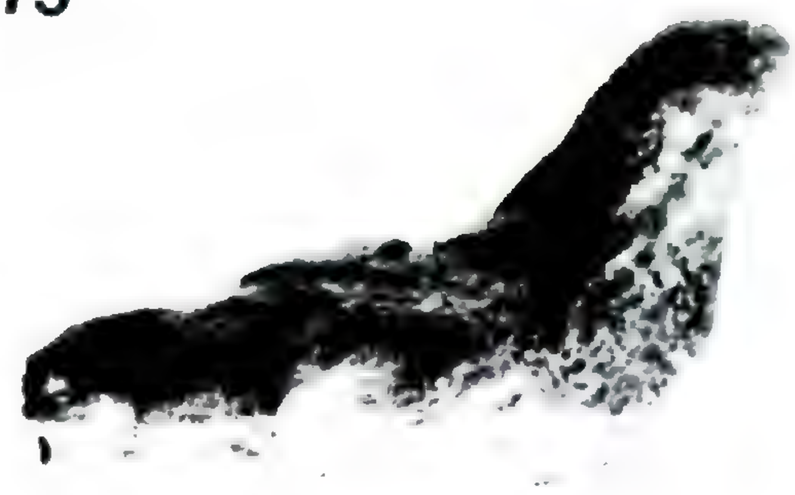

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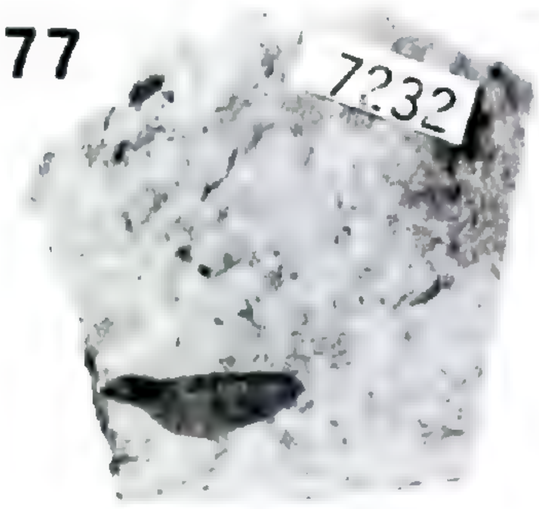

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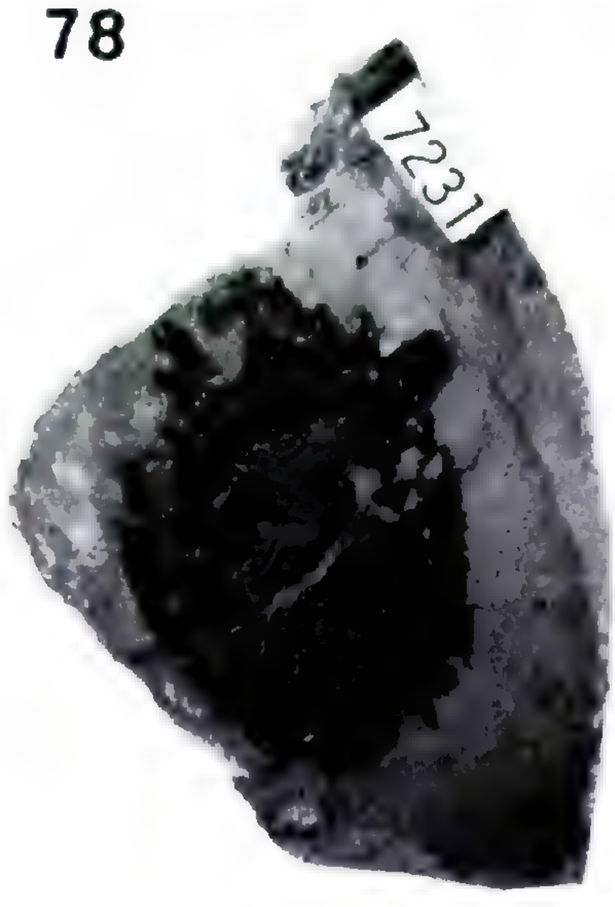

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homeotypes 7228–7230, 7235–7238, 7176, 7245; Bull Run, Nevada: U.C. Mus. Pal., hypotypes 7231–7232.

Subsect. *Oocarpae*

This alliance now occurs in California, southwest Oregon, and in Mexico. The California taxa, *P. muricata* D. Don, *P. radiata* D. Don, and *P. remorata* Mason form discontinuous populations along the central and southern California coast, whereas *P. attenuata* Lemmon has a scattered distribution in the interior. Those in Mexico, *P. greggii* Engelm., *P. oocarpa* Schiede, *P. patula* Schiede, and *P. pringlei* Shaw, are in the Sierra Madre Occidental and Oriental, and with *P. oocarpa* ranging south into Nicaragua (see maps in Critchfield and Little, 1966).

Pinus burtii Miller, Torrey Bot. Club Bull. 105: 93–97, figs. 1–9, 1978. TYPE: U.S.A. Massachusetts: Martha's Vineyard. U.S. Nat. Mus., holotype 222868. Figure 85.

This large cone comes from a Miocene greensand associated with vertebrate and invertebrate fossils at the north end of cliffs at Gay Head, Martha's Vineyard, Massachusetts (Miller, 1978). The mammals are of Early Miocene (Late Arikareean) age, or about 22 Ma according to D. Savage (pers. comm., 1984).

Based on its external and internal structure, Miller considered the cone a member of the *Oocarpae*. It differs from living species of the group in its long, cylindrical outline and large swollen apophyses. It differs from cones of the *P. radiata* populations in California, which are largely asymmetrical; *P. oocarpa* has smaller, more nearly ovate cones; *P. attenuata* has strongly hooked apophyses and is asymmetrical; and the Mexican species *P. patula, P. greggii,* and *P. pringleii* are more slender and tend to be asymmetrical, and the apophyses are subdued.

There may be a relationship between *P. burtii* and *P. O'Donnellii* Teixeira from the Miocene of Lisbon (see Gaussen, 1960, fig. 365: 1). If so, this would be another Miocene trans-Atlantic link.

The occurrence of a member of *Oocarpae* in the eastern United States provides an additional link with the upland flora of the Sierra Madre Oriental, a distribution discussed by others (Harshberger, 1911; Axelrod, 1960: 267–269; Graham, 1973; Greller & Rachele, 1983).

Pinus celetomensis Axelrod, sp. nov. TYPE: U.S.A. Nevada: Celetom Quarry 25 km east of Reno. U.C. Mus. Pal., holotype 7233. Figure 86.

Cone large, elliptic-ovate in outline, fully 14–15 cm long, 7.5 cm broad; base obtuse, tip acute; 10 and 13 rows of scales, those in middle 1.5–1.7 cm broad and 8–9 mm high, swollen, broadly rounded, asymmetrical and upcurved; apophyses strongly reflexed proximally and flattened on outer (anterior) side, less so distally; umbo centro-mucronate, the mucro very small, scarcely 1 mm long.

Discussion. This appears to be a new species of Subsect. *Oocarpae*. The cone is of the average size of the Año Nuevo population of *P. radiata*. It differs from *P. radiata* cones of this size in that the fossil is elliptic-ovate, not ovate, the apophyses are swollen to the distal end of the cone rather than being confined chiefly to its upper third or half. In addition, the apophyses are more flattened throughout and are reflexed proximally in the fossil; in *P. radiata* the apophyses are more evenly rounded and hence unlike the fossil.

This cone seems intermediate between those produced by *P. radiata* and *P. attenuata*. It differs from cones of *P. attenuata* in that the apophyses are not sharply acute or hooked. Whether the present specimen represents a form transitional between *P. radiata* and *P. attenuata* can only be determined when additional fossil specimens become available.

Pinus celetomensis was adapted to an interior, subhumid climate as judged from the composition of the nearby Purple Mountain flora which

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FIGURES 74–84.—74. *Pinus pieperi* Dorf. Mount Eden, California. U.C. Mus. Pal., hypotype 7227. Latest Miocene, 5–6 Ma. Water-worm cone.—75, 76. *Pinus hazeni* Axelrod. Mount Eden, California. U.C. Mus. Pal., hypotypes 7225, 7226. Latest Miocene, 5–6 Ma.—77, 78. *Pinus alvordensis* Axelrod. Bull Run, Nevada. U.C. Mus. Pal., hypotypes 7232, 7231. Late Eocene, 40 Ma.—79–82. *Pinus alvordensis* Axelrod. Creede, Colorado. U.C. Mus. Pal., hypotypes 7174, 7175, 7173, 7228. Latest Oligocene, 26.5 Ma.—83, 84. *Pinus alvordensis* Axelrod. Creede, Colorado. U. Colo. Mus., hypotypes 19706, 19707. Latest Oligocene, 26.5 Ma.

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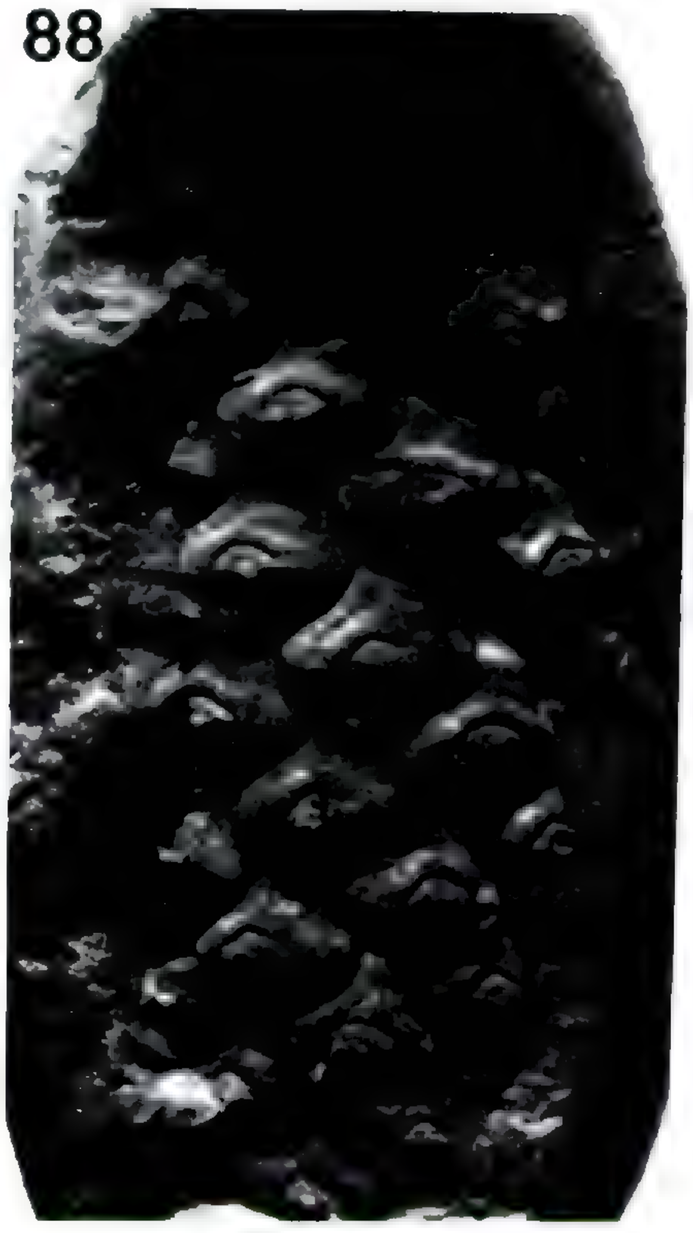

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represents vegetation in the ecotone between broadleaved sclerophyll forest and mixed conifer forest (Axelrod, 1976).

Pinus diegensis Axelrod & DeMéré. San Diego Soc. Nat. Hist. Trans. 20(15): 291, figs. 6A–B, 7A–B, 1984. TYPE: U.S.A. California: San Diego Formation. Holotype SDSNH 25135, paratypes 25110, 25136, 25137.

This recently-described pine of the *P. radiata* alliance is from Chula Vista, near San Diego, California. The species produced cones much like the present population *P. binata* on Guadalupe Island. The cones show considerable variation in size, symmetry, and apophyses development, as noted earlier by Howell (1941). The occurrence of such a pine on the mainland suggests that the insular species did not originate in isolation, and that it may have been ancestral to the present California populations at Monterey, Año Nuevo, and Cambria.

Pinus lawsoniana Axelrod, *in* R. N. Philbrick (ed.), Sympos. Biology of California Islands, p. 115, pl. 1, figs. 1, 2, 1967. TYPE: U.S.A. California: Old Forest Soil on Mussell Rock. U.C. Mus. Pal., holotype 20533, paratype 20534. Figures 90, 91.

Pinus masonii Dorf., Carnegie Inst. Wash. Publ. 412: 70, pl. 5, fig. 6 only, 1930.
Pinus pretuberculata Axelrod, Carnegie Inst. Wash. Publ. 476: 166, pl. 3, fig. 3 only, 1937.

Cones similar to those of *Pinus radiata* D. Don occur in rocks about 5–6 Ma old at Mussel Rock, on the outer coast south of San Francisco. They were recovered there by A. C. Lawson in 1893 from an old forest soil that rests on Jurassic diabase and *underlies* the marine Merced Formation. Similar cones are in the Mount Eden flora (Axelrod, 1937, pl. 3, fig. 3) dated at 5–6 Ma, and the Lower Pico Formation about 3 Ma old (Dorf, 1930, pl. 5, fig. 6).

Cones in the Chula Vista Formation south of San Diego are allied but were named *P. diegensis* Axelrod & DeMéré (1984) because they exhibit variation most like cones produced by the Guadalupe Island population. The specimens from Mussel Rock and Mount Eden seem more similar to those of the present Monterey population.

Occurrence. Mt. Eden, California: Mus. Nat. Hist. Los Angeles, hypotype L-1306;1014/688; Pico, California: U.C. Mus. Pal., hypotype 307.

Pinus pretuberculata Axelrod, Carnegie Inst. Wash. Publ. 476: 166, pl. 3, fig. 4 only, 1937. TYPE: U.S.A. California: Mount Eden. Nat. Hist. Mus., Los Angeles Co., lectotype 1014/696. Figures 87, 89.

Pinus pretuberculata Axelrod. Condit, Carnegie Inst. Wash. Publ. 553: 74, pl. 14, fig. 1, 1944; Axelrod, Univ. Calif. Publ. Geol. Sci. 34: 127, pl. 18, figs. 3–4, 11–13, 1958.

Discussion. Cones of this species have been recorded from the Mount Eden flora, southern California (Axelrod, 1937), the Table Mountain flora from the central Sierran foothills (Condit, 1944), and the Verdi flora of western Nevada (Axelrod, 1958). The Table Mountain flora is well dated at 12 Ma, the Mount Eden and Verdi are 5–6 Ma old. These records illustrate that the species had a wider distribution than its modern derivative, *P. attenuata* Lemmon, consistent with its new record at Celetom Quarry, Nevada.

The Celetom record, from diatomite in the lower part of the Coal Valley Formation, consists of the upper half of a cone estimated to have been 12 cm long and 6 cm broad at its widest part. There are 9 × 6 rows of scales preserved, the apophyses are conical, swollen, upswept to reflexed, and excentro-mucronate. The inside face (posterior) of the cone is missing, but there is evidence of smaller cone scales on the outer left margin so that it is apparent that the cone is asymmetrical. The cone scales are marked by prominent ridges on the outer sides so that in cross-section they are generally rhombic.

This cone appears to be typical of populations in the Sierra Nevada to the west, and especially

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FIGURES 85–89.—85. *Pinus burtii* Miller. Martha's Vineyard, Mass. U.S. Nat. Mus., holotype 222868. Early Miocene, ca. 22 Ma. (From Miller, 1978.)—86. *Pinus celetomensis* Axelrod, sp. nov. Celetom Quarry, 30 km E. of Reno, Nevada. U.C. Mus. Pal., holotype 7233. Late Miocene, 12 Ma.—87. *Pinus pretuberculata* Axelrod. Celetom Quarry, 30 km E. of Reno, Nevada. U.C. Mus. Pal., hypotype 7234. Late Miocene, 12 Ma.—88. *Pinus tiptoniana* Chaney & Axelrod. Tipton, Oregon. U.C. Mus. Pal., lectotype 129. Middle Miocene, 15 Ma. (Previously figured by Chaney & Axelrod, 1959.)—89. *Pinus pretuberculata* Axelrod. Table Mountain, California. U.C. Mus. Pal., hypotype 2720. Late Miocene, 12 Ma. (From Condit, 1944.)

FIGURES 90, 91.—90. *Pinus lawsoniana* Axelrod. Mussel Rock, S. of San Francisco, in forest soil below basal Merced Formation. U.C. Mus. Pal., holotype 20533. Late Miocene, ca. 5–6 Ma. (From Axelrod, 1967a.)—91. *Pinus lawsoniana* Axelrod. Mussel Rock, S. of San Francisco, in forest soil below basal Merced Formation. U.C. Mus. Pal., paratype 20534. Late Miocene, ca. 5–6 Ma. (From Axelrod, 1967a.)

to those in southern California that have more prominent apophyses. The modern *P. attenuata* occurs in the lower part of the forest belt, often forming nearly pure stands where it has been disturbed by fire. The species ranges discontinuously from southwestern Oregon into northern Baja California. In the south, it is regularly adjacent to the upper chaparral belt at the forest margin.

Occurrence. Table Mt.: U.C. Mus. Pal., hypotype 2720; Verdi, Nevada: MUC. Mus. Pal., hypotypes 1972–1975, homeotype 1971; Celetom Quarry, Nevada: U.C. Mus. Pal., hypotype 7234.

Pinus masonii Dorf, Carnegie Inst. Wash. Publ. 412: 70, pl. 5, figs. 4, 5 (not fig. 6 which is *P. lawsoniana* Axelrod), 1930. TYPE: U.S.A. California: Merced. U.C. Mus. Pal., holotype 308, paratype 306. Figure 94.

Pinus masonii Dorf. Axelrod, *in* R. N. Philbrick (ed.), Sympos. Biology of California Islands, p. 117, pl. 5, figs. 1–2, 4–5; pl. 6, fig. 2, 1967. Axelrod, Univ. Calif. Publ. Geol. Sci. 120: 39, pl. 12, figs. 1–4, 1980.

This pine, rather rare in pre-Pleistocene coastal deposits of California, has cones similar to those of *P. muricata* D. Don., now distributed discontinuously from the north coast of California southward into northern Baja California near Eréndira. Over this broad area the scattered populations are represented by three varieties (Axelrod, 1983a).

Its known fossil records are in the Lower and Upper Merced Formations on the coast south of San Francisco (Dorf, 1930; Axelrod, 1967, 1980), in the upper part of the Lower Pico Formation on the coast west of Ventura (Dorf, 1930), and in the Upper Pico Formation north of Santa Paula (Axelrod, 1967). The oldest of these records in the basal Merced Formation, is about 5 Ma.

Occurrence. Lower Pico, California: hypotypes 12738, 20380; Upper Pico, California: hypotype 20380.

Pinus tiptoniana Chaney & Axelrod, Carnegie Inst. Wash. Publ. 617: 142, pl. 13, figs. 3–6, 1959. TYPE: U.S.A. Oregon: Blue Mts. U.C. Mus. Pal., lectotype 129, paratypes 128, 643, 2866, 2867, 2869, homeotypes 642–644, 2868, 2870–2871. Figure 88.

This pine from the Blue Mountains flora, eastern Oregon, occurs in diatomaceous sediments interbedded with basalts of the Columbia River Lava Group. The fossil was compared initially with *Pinus halepensis* Miller, which it does resemble. However, comparison with cones in the collection at the Institute of Forest Genetics, Placerville, shows that *P. tiptoniana* is a member of the *Oocarpae*. This is indicated by the umbo, which is centro-mucronate, whereas in *P. halepensis* it is excentro-mucronate. *Pinus tiptoniana* appears to be an extinct species of the group, differing from those most nearly allied to it, e.g., *P. patula* Scheide & Deppe and *P. pringlei* Shaw, in having needles in 2s, and the fossil cones appear to be more nearly symmetrical as judged from the incomplete specimens. These modern pines allied to *P. tiptoniana* occur in the Sierra Madre Oriental, Mexico, generally at middle elevations in woodlands and forests adapted to a climate of high equability and ample summer rain.

PLEISTOCENE *OOCARPAE* FROM COASTAL CALIFORNIA

The following is a listing of younger records of *Oocarpae* from coastal California. Some of these deposits (e.g., Carpinteria, Pt. Sal) are (were) especially rich in cones that accumulated on floodplains. This is because the cones were not dispersed as widely by currents as in the case of the rare cone records from most marine deposits.

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FIGURES 92–94.—92. *Pinus radiata* D. Don. Santa Barbara Formation, Veronica Springs Quarry, Santa Barbara, Calif. Santa Barbara Mus. Nat. Hist., hypotype 473. Early Pleistocene, ca. 1 Ma. A cluster of four cones. (Previously figured by Axelrod, 1980.)—93. *Pinus muricata* D. Don. Upper Merced Formation, S. of San Francisco. U.C. Mus. Pal., hypotype 159. Early Pleistocene, ca. 1 Ma. (Previously figured by Mason, 1932 and Dorf, 1930.)—94. *Pinus masonii* Dorf. Lower Merced Formation, S. of San Francisco, Calif. U.C. Mus. Pal., hypotype 20532. Pliocene, ca. 3. Ma. (Previously figured by Axelrod, 1967.)

FIGURES 95–103. *Pinus muricata* D. Don, var. *borealis* Axelrod. Near Point Sal, Santa Barbara Co., Calif. U.C. Mus. Pal., hypotypes 20400–20408. Late Pleistocene, ca. 26,700 ± 800 years B.P. (From Axelrod, 1967.)

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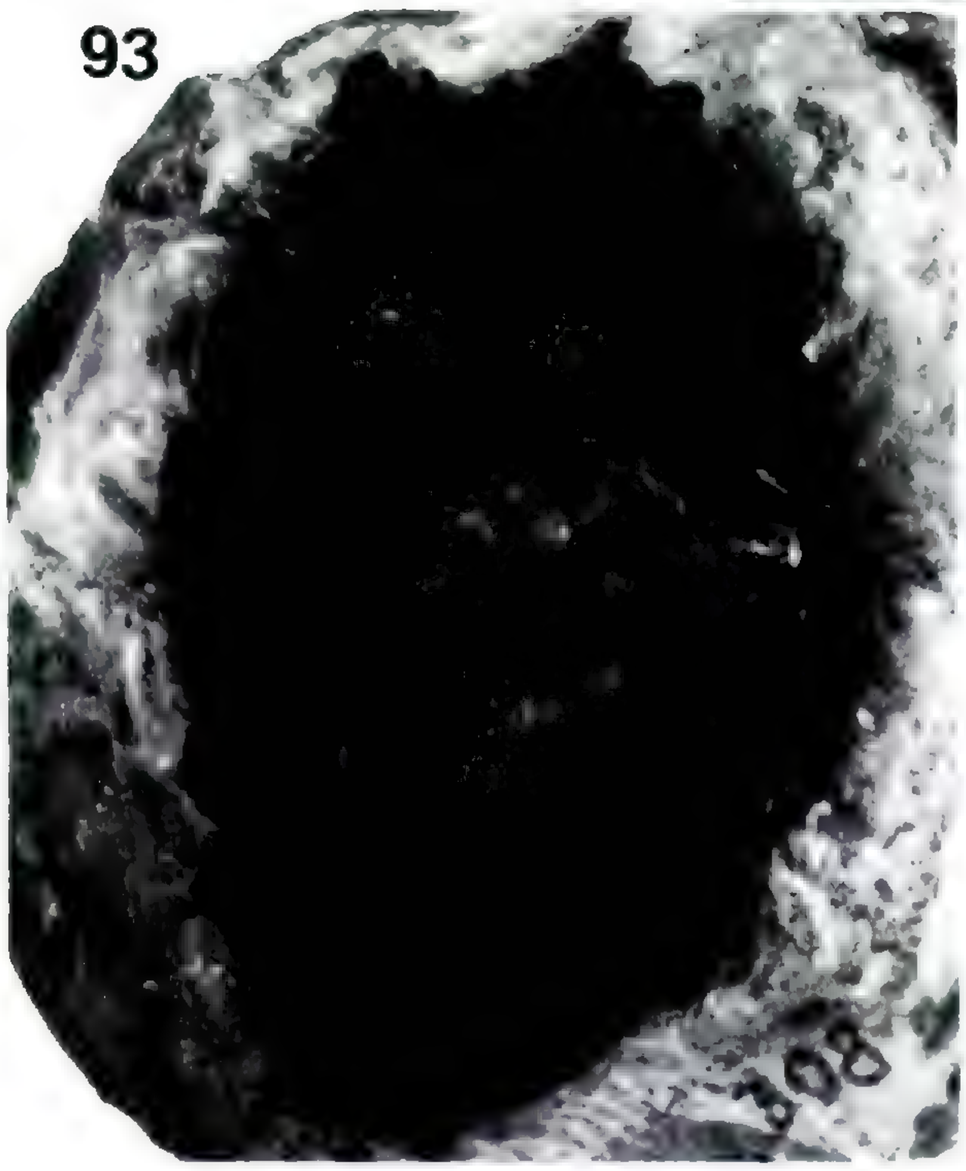
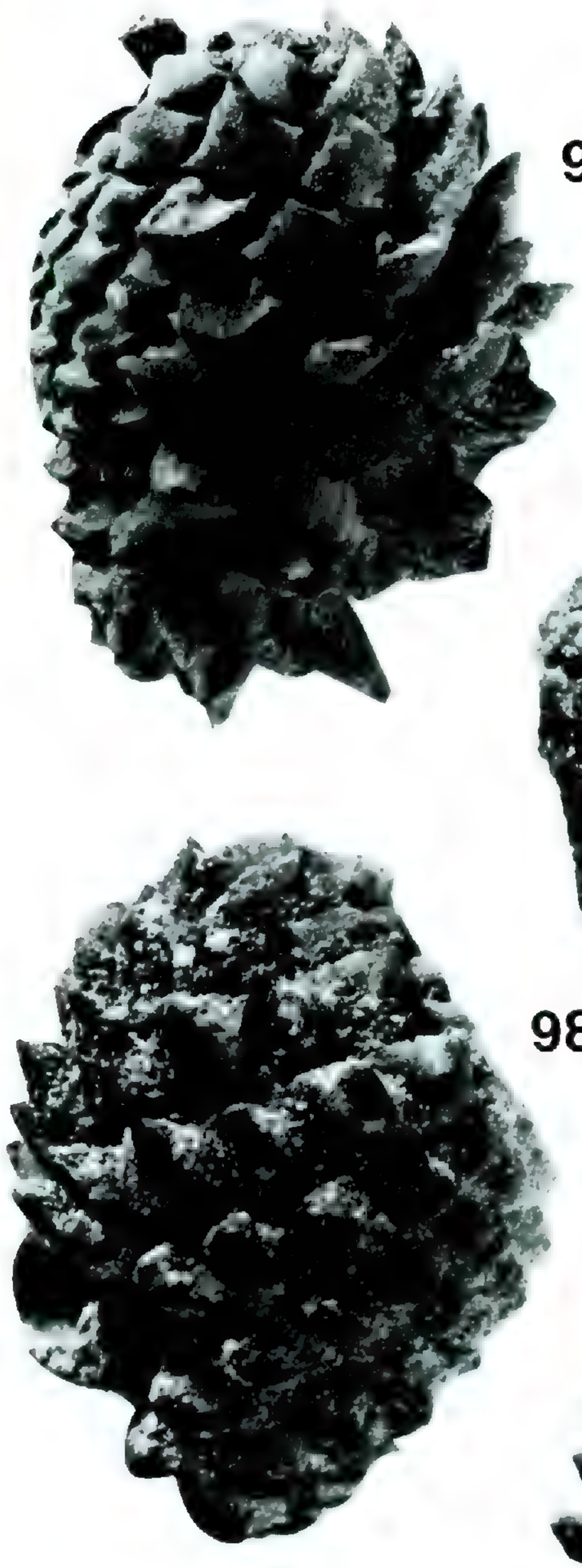


94



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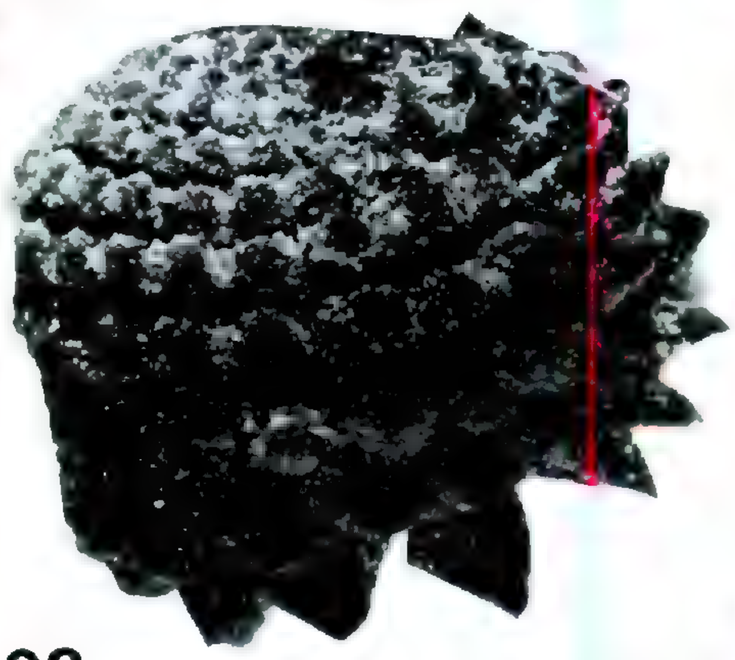

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FIGURES 104–108.—104, 105. *Pinus remorata* Mason. Century City, Los Angeles. U.C. Mus. Pal., hypotypes 5841, 5840. Plio-Pleistocene transition, ca. 2 Ma.—106. *Pinus remorata* Mason. Santa Cruz Island, Willow Creek. U.C. Mus. Pal., hypotype 5839. Late Pleistocene, 14,200 ± 250 years B.P.—107. *Pinus remorata* Mason. Near Point Sal, Santa Barbara Co., Calif. U.C. Mus. Pal., hypotype 5840. Late Pleistocene, 26,700 ± 800 years B.P.—108. *Pinus remorata* Mason. Carpinteria, Calif. Santa Barbara Mus. Nat. Hist., hypotype 474. Late Pleistocene, older than 38,000 years B.P. (All specimens previously figured by Axelrod, 1980.)

Pinus attenuata Lemmon.
Late Pleistocene
Oakland (Metcalf, 1923).
Early Pleistocene
Seacliff (Axelrod, 1983); Signal Hill (Mason, 1932; Axelrod, 1967).

Pinus muricata D. Don. Figures 93, 95–103.
Late Pleistocene
var. *muricata*. Rancho La Brea (Mason, 1927).
var. *borealis*. Millerton (Mason, 1934); Carpinteria (Chaney & Mason, 1933; Axelrod, 1967, 1980).
Early Pleistocene
var. *muricata*. Seacliff (Axelrod, 1983); Wilmington (Axelrod, 1967).
var. *stantonii*. Seacliff (Axelrod, 1983).

Pinus radiata D. Don. Figure 92.
Late Pleistocene
Millerton (Mason, 1934); Drakes Bay (Axelrod, 1980, 1983); Thornton Beach (Axelrod, 1967); Pt. Sal (Axelrod, 1967); Carpinteria (Chaney & Mason, 1933); Santa Rosa I. (Axelrod, 1980); Rancho La Brea (Mason, 1927; Warter, 1976); Little Sur (Langenheim & Durham, 1963).
Early Pleistocene
Potrero Canyon (Axelrod, 1967); Seacliff (Axelrod, 1983); Century City (Axelrod, 1980); Spring Valley Lake (Axelrod, 1967); Veronica Springs (Axelrod, 1980).

Pinus remorata Mason. Figures 104–108.
Late Pleistocene
Carpinteria (Chaney & Mason, 1933; Axelrod, 1980); Santa Cruz I. (Chaney & Mason, 1930); Pt. Sal (Axelrod, 1967).
Early Pleistocene
Potrero Canyon (Axelrod, 1967); Century City (Axelrod, 1980), Seacliff (Axelrod, 1983).

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A HISTORICAL SKETCH OF THE VEGETATION OF THE MOJAVE AND COLORADO DESERTS OF THE AMERICAN SOUTHWEST[1]

ROBERT F. THORNE[2]

ABSTRACT

The Mojave and Colorado Deserts of the American Southwest are geologically recent in origin, resulting primarily from the rain-shadow caused by the Late Pliocene-Pleistocene elevation of the Sierra Nevada, Transverse, and Peninsular ranges. Their age thus is perhaps two to three million years. The present vegetation is even more recent, largely Holocene in origin, and still evolving. During the last, Wisconsin, glacial episode the California deserts were well supplied with huge, deep lakes and large streams and an open woodland, possibly grassy, supporting numerous large mammals, now mostly extinct. The desert flora, however, is in large part more ancient, having been assembled since early Paleogene time from many sources. Most of the perennials are probably former members of the Madro-Tertiary Geoflora that dominated southern California and adjacent areas during the Tertiary. They are species of dry habitats preadapted to long periods of drought, hot, dry summers, and cool, wet winters and thus able to populate and adapt to the varied desert habitats when they became available. They survived cool, pluvial, glacial periods by migration southward or to lower elevations. Some elements of the American southwestern desert flora are derived from Mexico, South America, central Asia, and a few possibly from North Africa and the Mediterranean region by overland immigration or long distance dispersal. In some instances this was aided by changing ocean size due to continental movement, glacial sea-level lowering, and to changes in oceanic-current patterns. Some desert plants, at least some of the ephemerals, may well be of very recent, even Holocene, origin in our arid Southwest.

Those of us without much geological training, in view of our own brief life span, tend to think of large-scale features of the landscape as rather permanent, thus very ancient. Yet geologists assure us that large lakes, islands, mountains, and the deserts behind them are relatively ephemeral in the geological time scale. Our southwestern deserts are no exception. The existing regional deserts or semi-deserts are geologically recent, possibly only a couple of million years old, at least as we know them today. They are essentially products of the late Pliocene-Pleistocene elevation of the Sierra Nevada, Transverse, and Peninsular ranges in southern California, which created a huge rain-shadow to the east. Thus, most of the moisture gleaned from the Pacific Ocean by the prevailing westerly winds precipitated on the western slopes of the ranges. As the air masses descended the transmontane slopes, they heated up adiabatically and became a drying force.

REGIONAL GEOLOGY

It is impossible to obtain exact dating for incidents of regional uplift. Often we must rely heavily upon circumstantial evidence presented by juxtaposition of strata, by radiometric dating of volcanic rocks, or by fossil floras and faunas of the region. When properly dated, fossil assemblages of plants and animals allow us to infer much about the past vegetation and climatic conditions of periods in question and the changes that have taken place. Leaves that are mostly large, entire-margined, and evergreen indicate warm-temperate to tropical forest conditions, and large numbers of grazing mammals presumably require rather extensive savannas or open grasslands.

Oakeshott (1971) reported that radiometric dating of volcanic rocks indicated "that the intensive faulting of the eastern side of the Sierra (accompanied by uplift and westward tilting) began about 2.5 million years ago." Paleoclimatic evidence from fossil floras of the region indicates that until that time the Sierra Nevada was a range with only low to moderate relief and that it became a major topographic barrier after the close of the Pliocene (Axelrod, 1962; Axelrod & Ting, 1960). From reconstructed stream profiles and paleobotanical evidence Axelrod estimated total

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post-Pliocene uplift in the Yosemite region at 1,980–2,135 m. Likewise he placed total post-Pliocene displacement at Donner Summit at about 1,525 m, at Carson Pass at about 2,135 m, and at Mount Whitney at about 2,745 m (Axelrod, 1962). Bachman (1978) estimated that "Relative uplift between Owens Valley and the White-Inyo Mountains may have been as much as 2,300 m during the past 2.3 m.y."

According to Foster (1980) the central Transverse Ranges during the late Cenozoic Era evolved from an area of low relief to a region of rugged high mountains. He estimated that the "Uplift of the San Gabriel Mountains began at least in Crowder time, 4–2 m.y.b.p., and possibly earlier. Erosion followed and uplift renewed as the upward coarsening Harold and Shoemaker deposits formed in Rancholabrean time, approximately 600,000–100,000? yr.b.p." He also believed that the San Bernardino Mountains had only moderate relief in late Hemphillian-Blancan time [Late Miocene, 5–8 Ma], but were worn down to a pediment (an area of low relief) by Crowder time (Plio-Pleistocene). The elevation of the San Bernardino Mts. by Upper Pleistocene time is attested to by the glacial deposits on San Gorgonio Peak.

Because folded and faulted strata of Lower Pleistocene time in the Ventura Basin portion of the western Transverse Ranges are overlain unconformably by upper Pleistocene beds, Oakeshott (1971) concluded that "one of the most violent mountain-building pulses was clearly in the middle Pleistocene." In reference to the San Gabriel Mountains, Oakeshott described the great mid-Pleistocene orogeny as "very widespread, involving uplift, tight folding, major faulting, and general destruction of the Tertiary basins by mountain-building processes . . . . Crustal movements have continued to the present day." Bull (1978) estimated that uplift rates along the south side of the San Gabriel Mountains appear to average about 1 to 3 m per 1,000 years. Indeed the youthful ruggedness of the range and the all too-frequent earthquakes in the area attest to the continued mountain building.

The fossil Soboba Flora (Axelrod, 1980a) west of the San Jacinto Mountains of southern California is now dated at about 1.75 Ma in Early Pleistocene time. From the plant species and plant communities represented in the fossil flora, Axelrod (1966) believed that the nearby San Jacinto Peak then stood at about 2,135 m compared to its 3,302 m today. Axelrod estimated that the major Transverse and Peninsular ranges then had elevations about half those of the present day. It would appear that the San Jacinto Mountains, at least, gained nearly 1,220 m in elevation since the Early Pleistocene.

In the Colorado Desert (i.e., the Lower Colorado River Valley subdivision of the Sonoran Desert) of extreme southern California the Salton Basin shows convincing evidence, according to Oakeshott (1971), of "great vertical displacements in late geologic history . . . displacement within the Salton Trough is going on very rapidly." Linday and Lindsay (1978), discussing the Pleistocene vertical faulting of the Peninsular Range ridges on the western side of the Salton Trough, believed that the "resulting 'rain-shadow' effect, coupled with drying of California climates in general, caused an arid climate to develop here, and a desert evolved about 20,000 years ago." Admitting the problematic accuracy of some of these dates, one must still conclude that the California regional deserts are indeed geologically a very recent phenomenon.

During Late Wisconsin and Holocene Transition time, under a cool, moist, pluvial climate, the California deserts were supplied with an extensive river and lake system. It is estimated that as much as 20 percent of the Mojave Desert was covered by fresh water to an average depth of 30 m (G. Jefferson, pers. comm.). Searles Lake, for example, was estimated at 132 m deep and 26 km long, Lake Panamint at 280 m deep and 100 km long, Lake Manly of Death Valley at 275 m deep and 175–240 km long, and Lake Manix at 60 m deep and 515–775 sq km in area (Blanc & Cleveland, 1961; Oakeshott, 1971). Until it disappeared about 500 years ago, Lake Cahuilla, a predecessor of the Salton Sea, filled the Salton Basin with about 5,180 sq km of fresh water (Lindsay & Lindsay, 1978).

Tertiary Vegetation in Southern California

It may be of some interest to examine the past vegetation of our present deserts and adjacent regions of southern California. Presently, according to my moderately liberal classification, there are 140 angiosperm families indigenous in California. The state had a much richer family representation in the Tertiary. Both mega- and microfossils indicate that at least 40 more angiosperm families were present in California during Late Cretaceous and Tertiary time (not to

mention at least nine additional families of pteridophytes and gymnosperms) (Potbury, 1935; MacGinitie, 1937, 1941; Axelrod, 1950e, 1958, 1973; Drugg, 1967; Jarzen, 1980; Page, 1981) but have been eliminated from the flora by changed climatic conditions. Presumably other, especially herbaceous, families failed to be fossilized or to be recognized. Many of these now exotic families are found today to the south in Baja California or east in southern Arizona, often near California's borders, such as the Malpighiaceae, Menispermaceae, Moroideae, Passifloraceae, Sapindaceae, and Sapotaceae. Others can be found in the Cape Region of Baja California, subtropical Sonora or Sinaloa, or farther south in Mexico, as Aquifoliaceae, Bombacaceae, Buxaceae, Chloranthaceae, Chrysobalanaceae, Clethraceae, Combretaceae, Dilleniaceae, Ebenaceae, Flacourtiaceae, Gunneraceae, Hamamelidaceae, Icacinaceae, Illiciaceae, Magnoliaceae, Meliaceae, Myrtaceae, Nelumbonaceae, Nyssaceae, Proteaceae, Sabiaceae, Symplocaceae, Theaceae, and Tiliaceae. Others today find refuge in eastern Asia, as Alangiaceae, Cercidiphyllaceae, and Trapaceae, or in Australia, as Alangiaceae and Eupomatiaceae.

PALEOGENE

Early in the Tertiary the topography and climate of California was very different from the present, and tropical seas covered much of coastal and central California. Much of southern California west of the San Andreas fault had not yet joined the state, being then part of Baja California, which in turn was part of mainland Mexico, the Gulf of California not yet having been formed. Topography was low and rolling, and temperate (cloud) to subtropical rainforest apparently covered the coast, and subtropical savanna and dry tropical (short-tree) forest probably covered much of the interior, possibly with oak woodland on the highlands above. Farther north a lush evergreen-deciduous hardwood forest similar to that found today in southeastern China, vegetated much of the state's interior (Potbury, 1935; MacGinitie, 1937, 1941; Axelrod, 1950e, 1958, 1973, 1979; Raven & Axelrod, 1977).

MIOCENE

During the long Miocene Epoch the region that presently forms southern California supported in coastal areas and on moister slopes inland a generalized woodland of sclerophyllous trees dominated by live oaks (*Quercus*) and laurels (*Persea, Ocotea, Nectandra,* and *Umbellularia*), but with a rich assemblage of other genera as well, including *Acer, Annona, Bumelia, Cedrela, Clethra, Dioon, Ficus, Ilex, Juglans, Laurocerasus, Lithocarpus, Lyonothamnus, Magnolia, Myrica, Pinus, Platanus, Populus, Prunus, Sabal,* and *Sapindus,* as found variously in the Anaverde, Mint Canyon, Mount Eden, Puente, Piru Gorge, and Temblor floras (Axelrod, 1937, 1939, 1940, 1950b, 1950c, 1950d, 1973). This vegetation thrived on ample summer rainfall and a mild climate with no frost in winter. As Miocene climate became drier and cooler, many of the genera were forced south out of mainland California. Those genera left in Alta California are found now scattered in island oak woodland, riparian woodlands, southern mixed evergreen forest, or other more mesic communities. Closed-cone conifer forests (dominated by pines equivalent to modern *Pinus muricata* D. Don and *P. radiata* D. Don) occupied sheltered slopes by the ocean (Axelrod, 1980b).

In the drier interior, particularly in the present desert regions, oak woodland covered the lowlands with riparian woodland following the waterways. Characteristic of the woodland-savannas were *Quercus, Pinus, Cupressus, Aesculus, Juglans,* and *Robinia* and of the riparian woodlands *Acer, Brahea, Bumelia, Celtis, Juglans, Lyonothamnus, Platanus, Populus, Sabal, Salix,* and *Sapindus.* Chaparral occupied the well-drained slopes, short-tree forest the moister slopes, and subtropical thornscrub the rocky, lower, drier slopes. All of these communities, like the coastal sagescrub (Axelrod, 1978), closed-cone conifer forest (Axelrod, 1980b), and oak-laurel woodland, belong to the Madro-Tertiary flora, which had apparently evolved on dry sites during the Eocene out of the warm-temperate-subtropical coastal rainforests through capacity to endure dry, cool conditions. This southern flora, with more evergreen, thicker, and smaller leaves than the Arcto-Tertiary Flora to the north, soon spread in Oligocene and Miocene time over much of the drier Southwest (Axelrod, 1950a, 1950e, 1958, 1973, 1979).

Most exotic to Californians would be the subtropical thornscrub, retained now only in part in the microphyllous woodland and mixed desert-scrub of the warmer Colorado Desert. It contained many trees and shrubs with small leaves or leaflets, and often with spines, of such genera as *Acacia, Bursera, Castela, Celtis, Cercidium,*

Colubrina, Condalia, Crossosoma, Dodonaea, Euphorbia, Eysenhardtia, Fouquieria, Jatropha, Karwinskia, Leucaena, Lycium, Lysiloma, Mahonia, Olneya, Pachycormus, Piscidia, Pithecellobium, Prosopis, Prunus, Psorothamnus, Randia, Thouinia, Xanthoxylum, and *Ziziphus,* the palms *Brahea, Sabal,* and *Washingtonia,* the arborescent *Nolina,* the vines *Cardiospermum* and *Passiflora,* and such larger leaved genera of trees as *Diospyros, Ficus, Quercus,* and *Trichilia* as found in the Anaverde, Mint Canyon, Mount Eden, and Tehachapi floras (Axelrod, 1937, 1950a, 1950b, 1950c, 1973). Although it required adequate summer rainfall and mild winters, the thornscrub occupied semiarid slopes. This vegetation today is best developed south of the border where rain falls mostly in the warm season and frosts are rare or absent (*Trichilia* species, for example, require such freedom from frost).

Late Miocene-Pliocene-Early Pleistocene

The Baja California peninsula is believed to have begun its separation from continental Mexico in Middle Miocene time, but with most of the rifting and spreading taking place in the last 6–4 Ma, with movement northwestward of perhaps 260 km (Larson et al., 1968; Seyfert & Sirkin, 1979). What is now southern California west of the San Andreas Fault likewise moved northwestward in Early Pliocene about 300 km in the last five Ma (Atwood, 1970). Right-slip movements offshore have apparently displaced the California islands 120–160 km also northwestward (Axelrod, 1979).

Precipitation decreased in late Miocene with apparent elimination of the short-tree forest from the present desert areas of southern California and impoverishment of the oak-conifer woodland and thornscrub, as indicated by the Ricardo and Anaverde floras from the western Mojave (Axelrod, 1939, 1950c, 1979). Because aridity peaked about 5–8 Ma, it is likely too that semidesert patches increased in number and extent in drier areas of southern California toward the close of the Miocene.

Previous to Pliocene time the sclerophyllous woodland that blanketed the present deserts of southern California, along with a similar flora over most of the area, spoke for a single Mojavean phytogeographic province over what are now the Mojave and Colorado deserts. With the elevation of the Mojave area during the Pliocene, the resulting colder climate eliminated most of the thornscrub and other more tropical elements from the Mojave highlands and replaced them largely with Great Basin taxa from the north. The lower, warmer Colorado Desert to the south formed then a distinct Coloradoan phytogeographic unit with many thornscrub and other subtropical taxa and a great diversity of life forms. For the most arid sites of the Colorado Desert a semidesert flora can be inferred (Axelrod, 1979).

In late Pliocene-Pleistocene time the elevation of the Sierran, Transverse, and Peninsular ranges, as discussed above, created the regional rain-shadow deserts of southern California. At the same time the increasingly colder California Current off the southern California coast restricted the summer rains farther south. Those floristic elements requiring summer precipitation and warmer winter temperatures were eliminated from the California deserts and found refuge in more southern divisions of the Sonoran Desert. From the various plant formations that had vegetated the present desert or adjacent areas those Madro-Tertiary species preadapted to arid desert conditions presumably moved directly or via arid pockets of semidesert vegetation into the open ecological niches to form the basis of our present desert flora during the Pleistocene interglacials and subsequent Holocene time. Some of the movements of the local vegetation during the last, Wisconsin, glacial episode and the postglacial period are discussed below.

Present Desert Vegetation

If our California deserts are largely of Late Pliocene-Pleistocene age, the desert plant communities are even more recent, having evolved from existing Madro-Tertiary plant formations as the desert-forming rain-shadows developed. These plant communities are of Holocene age, i.e., they acquired their present distribution and composition during the last 8,000–11,000 years since the retreat of the last, Wisconsin, episode of the numerous cycles, perhaps 19 or 20 according to Imbrie and Imbrie, (1979), of Pleistocene continental glaciation. The Wisconsin peaked from 21,000–11,000 years ago (as interpreted by Cole, 1982).

We have been treated to a relatively clear concept of the vegetation of the Great Basin, Mojave Desert, Colorado and other subdivisions of the Sonoran Desert since Wisconsin time through the efforts of many botanists and paleontologists.

Laudermilk and Munz (1938), Martin, Sabels, and Shutler (1961), and Martin and Sharrock (1964) have studied the coprolites of ground sloths, carnivores, and man. Martin (1964), Martin and Gray (1962), Martin and Mehringer (1965), Mehringer (1965, 1966), and Mehringer and Haynes (1965) have used pollen analysis to interpret Pleistocene and Holocene desert environments. Especially productive has been the study of packrat (*Neotoma*) middens by Wells and Jorgensen (1964), Wells and Berger (1967), Mehringer and Ferguson (1961), Van Devender and King (1971), Lanner and Van Devender 1974, Phillips and Van Devender (1974), King (1976), Van Devender (1976), Van Devender and Mead (1976), Wells (1976, 1983), Wells and Hunziker (1976), Van Devender and Spaulding (1979), Cole (1982), Wells and Woodcock (1985), Cole and Webb (1985), and Cole (1986). Dendrochronology has also been useful.

Apparently until early Holocene time (ca. 9,000 years ago), the Mojave Desert lowlands were vegetated by a coniferous woodland of low-statured junipers and pinyons, chiefly *Juniperus osteosperma* (Torrey) Little and *Pinus monophylla* Torrey & Frem., or solely of juniper, accompanied by *Yucca brevifolia* Engelm. in S. Watson, *Yucca whipplei* Torrey, *Coleogyne ramosissima* Torrey, and *Artemisia, Ephedra,* and *Opuntia* spp., and other xerophytes (Wells & Berger, 1967; King, 1976; Wells, 1983; Wells & Woodcock, 1985). Absent from these woodlands were such hot desert plants as *Larrea divaricata* Cav. and *Ambrosia dumosa* (A. Gray) Payne. The first *Neotoma* records of *Larrea* in the Mojave Desert are from the north side of the Ord Mountains about 7,400 years ago (Wells 1983) and from the Lucerne Valley side of the same range to the south at about 5,800 years ago (King, 1976). Vasek (1980) has estimated the oldest *Larrea* clones in the nearby Johnson Valley at about 7,800 years. Presumably the hot-desert species like *Larrea* found refuge during the glacials in the low, warm Colorado Desert (Wells & Berger, 1967). *Larrea* has been reported in Death Valley (Wells & Woodcock, 1985) no earlier than 1,990 + 160 years ago.

In a study of *Neotoma* middens in the very arid lower Colorado River Valley about Picacho Peak, Imperial County, California, at elevations of 245–300 m, Cole (1986) documented 12,500 years to the present of creosotebush desert scrub dominated by *Larrea divaricata, Encelia farinosa* A. Gray ex Torrey, and *Peucephyllum schottii* (A. Gray) A. Gray. He considered this hyperarid area to be a Pleistocene desert refugium. At this site Joshua tree, *Yucca brevifolia,* perhaps the most characteristic Mojave Desert species and now largely restricted to the Mojave, was present about 12,500 years ago, and associates, such as *Brickellia arguta* Robinson, *Chrysothamnus teretifolius* (Dur. & Hilg.) Hall, *Coleogyne ramosissima, Lycium cooperi* A. Gray, *Salvia mohavensis* Greene, and *Yucca whipplei* Torrey, none now known in the immediate area, were present into the early Holocene until nearly 10,000 years ago. The authors also mentioned late Wisconsin and early Holocene *Pinus monophylla* from as low as 460 m in the Tinajas Altas Mountains of Arizona and a more xeric juniper (probably *Juniperus californica* Carr.) woodland from 600 to 240 m in the Whipple, Chemihuevi, Tinajas Altas, and Butler mountains [until about 8,900 years ago, according to Van Devender (pers. comm.)].

In contrast, *Ambrosia dumosa, Fouquieria splendens* Engelm., and *Olneya tesota* A. Gray appeared in middens only less than 600 years old. Possibly these and other Sonoran, hot-desert plants requiring warm temperatures and summer rainfall, had found refuge farther south in the Arizona and Mexican portions of the Sonoran Desert, returning for short periods in each interglacial.

The Mojave Desert in turn served as a refuge for the cold-desert plants, as well as the pinyon-juniper woodlands, which in Holocene time returned to the Great Basin to become the dominant vegetation there. *Pinus flexilis* James and *P. longaeva* Engelm., now absent from Mojave Desert ranges, were recorded by *Neotoma* from the Clark Mountains about 20,000 years ago, with *P. longaeva* already absent and *P. flexilis* rare by 12,460 BP (Mehringer & Ferguson, 1969). Wells and Woodcock (1985) reported *Yucca whipplei* in Death Valley as early as 19,550 + 650 BP along with *Atriplex confertifolia* (Torrey & Frem.) S. Watson and *Opuntia basalaris,* and somewhat later (about 17,000 to 9,500 BP) *Chrysothamnus teretifolius, Purshia glandulosa* Curran, and *Haplopappus cuneatus* A. Gray. *Ambrosia dumosa* appeared there by 10,230 + 320 BP, but *Larrea* not until 1,990 BP.

The presence of large, grazing mammals, such as horses, camels, bison, and mammoth, and such browsers as mastodons and ground sloths in the Mojave Desert during the Pleistocene pluvial periods would seem to require that the coniferous

woodlands probably were well supplied with grasses and other edible herbage. The China Lake faunule included two species of camels, two horses, a bison, a mammoth, a deer, and such carnivores as the saber-toothed cat (*Smilodon*), a dire wolf, and a coyote (Fortsch, 1978). Fortsch designated it a Rancholabrean fauna, and cited one preliminary age determination of fossil ivory from a mammoth at 18,600 + 4,500 years BP. Davis and Panlaqui (1978) inferred from this faunule that Lake China could be reconstructed as a "shallow, wind-stirred, fresh water lake; marshes, sloughs and sluggish streams surrounding the lake; some gallery forests of lakeside trees. These aquatic habitats were surrounded, at times, by a tall-grass savanna . . . . However, during the heights of the stadials, the environmental background of Lake China was evidently a cold steppe with some xeric, desert forest such as juniper." The PaleoIndians, who were general foragers, preyed occasionally upon the large herbivores, and were considered by Davis and Panlaqui to be culturally and linguistically complex by 15,000 BP.

Another site of Late Wisconsin/Holocene Transition time, in which early American man is known to have overlapped with now extinct large herbivores, is the Lehner Mammoth site in southeastern Arizona, from which the fossil pollen was studied by Mehringer and Haynes (1965). Clovis fluted points, butchering tools, and charcoal were found there associated with the remains of mammoth, horse, tapir, and bison. Both grazing mammals and the pollen gave evidence of desert-grassland 11,200 years ago.

Packrat midden studies in Death Valley established a 1,200–1,500 m downward displacement of juniper woodland 13,000–19,000 years ago (Wells & Woodcock, 1985). Similar studies in the Grand Canyon have suggested up to a 1,000 m climatic depression during the full-glacial period (21,000–15,000 years ago) of most plant species, particularly in the juniper and blackbush scrub communities (Phillips & Van Devender, 1974; Cole, 1982). These findings support, at least for higher-elevation deserts, a model of latitudinal displacement of climate. King (1976) concluded that his packrat midden data from the Lucerne Valley of the Mojave Desert suggested a 365 m depression of *Juniperus osteosperma* woodland between 12,100 and 7,800 years ago. In a study of Neoglacial vegetation changes in Greenwater Valley near Death Valley, Cole and Webb (1984) found a downward shift of 50 to 100 m in plant communities during the past 500 years. Thus, the latitudinal and elevational movement of plant communities is still going on, along with the addition to and deletion of species from the communities. Our present desert plant communities are not only very recent, they are highly dynamic, indeed kaleidoscopic in content and location.

Origins of the California Desert Flora

The present California desert flora is largely composed of autochthonous elements from the Madro-Tertiary Geoflora that dominated southern California and adjacent areas throughout the Tertiary. Other, rarer floristic elements, also preadapted to long periods of drought, hot, dry summers, and cool, wet winters, have arrived from other parts of America and the rest of the world to complete the desert flora. These latter elements deserve some discussion.

In addition to the rather obvious Sonoran elements, Mexico has supplied many of the allochthonous floristic elements found in the California deserts. From their distribution and that of their closest relatives, it would appear that *Mortonia utahensis* (Cov.) Nelson (Prigge 1983), *Buddleja utahensis* Cov., *Yucca brevifolia, Y. schidigera* Roezl ex Ortgies, *Yucca whippleyi, Castela emoryi* (A. Gray) Moran & Felger, and *Pilostyles thurberi* A. Gray, among others, have arrived in California from the southeast, probably from the Chihuahuan Desert of northern Mexico. *Fouquieria splendens* Engelm., now very conspicuous in the Colorado and other subdivisions of the Sonoran Desert along with several of its congeners in Baja California, has most of its relatives in mainland Mexico, south to Oaxaca (Henrickson, 1972). Other possibly non-Sonoran Mexican immigrants are such plants as *Selinocarpus nevadensis* (Standley) Fowler & Turner, *Pholisma arenarium* Nutt. ex Hook., *P.* (*Ammobroma*) *sonorae* (Torrey ex A. Gray) Yatskievych, and *Proboscidea althaeifolia* (Benth.) Duchesne, all with strong relationships to the south with Mexican, but with no close Californian, relatives.

South America has surely supplied a number of California desert plants, not the least being the creosote-bush, *Larrea divaricata* Cav. [or *L. tridentata* (Sessé & Mociño ex DC.) Cov. for those who consider it a distinct species], surely the most widely distributed, abundant, and often dominant woody plant in the warm deserts of North America. The North American desert plant, so

closely similar to an Argentine species both morphologically and biochemically as to be probably conspecific with it, has differentiated cytogeographically since its arrival in North America (Wells & Hunziker, 1977). The Chihuahuan Desert race retains the ancestral diploid condition but the Sonoran and Mojave Deserts have derived tetraploid and hexaploid races respectively. The recent advent of *Larrea* in the Mojave Desert has been discussed above. Although *L. divaricata* has races in South America as far north as Peru, the North American races have closer biochemical affinity with the Argentine race. *Larrea* probably was carried to Mexico directly from Argentina or Chile by migrating birds, and subsequently moved from the Mexican deserts into the Californian deserts in late interglacial and Holocene time.

Other distinctive woody species with probable South American ancestry are *Frankenia salina* (Molina) I. M. Johnston, disjunct between western Mexico-California and Chile, the capparaceous *Koeberlinia spinosa* Zucc., disjunct between the North American Southwest and Bolivia, and *Atamisquea emarginata* Miers, disjunct between northwestern Mexico-Arizona and Argentina-Chile. The North American desert species of the oleaceous *Menodora,* mimosoid *Prosopis* and *Prosopidastrum,* and solanaceous *Lycium* and *Nicotiana* likewise have strong links with temperate South America. *Menodora* and *Lycium* have representatives as well in southern Africa, and *Nicotiana* also in Africa, Australia, and Polynesia. *Thamnosa* of the Rutaceae seems to be unrepresented in South America but does have species in southwestern Africa, the Horn of Africa, and Arabia. Possibly it followed migratory routes somewhat similar to those of *Menodora, Lycium,* and *Nicotiana* with subsequent loss of representation in temperate South America. In contrast, *Selinocarpus* of the Nyctaginaceae, mostly of the North American Southwest, has a species in Somalia, like *Thamnosma,* but no species in southern Africa or South America. Most of the desert herbaceous genera that have links to South America appear to have evolved in North America and to have been carried south to temperate South America relatively recently, no doubt also by migratory birds (Raven, 1963; Thorne, 1973).

The more northern elements of the California deserts have apparently entered the warmer deserts from the Great Basin Semidesert. The linkage of many of these genera seems to be strong with the arid areas of central Asia. Among the more prominent desert genera with a possible Asian origin are *Artemisia, Atriplex, Ceratoides* (*Eurotia*), *Kochia, Mahonia, Monolepis, Prunus* subg. *Amygdalus, Stipa,* and *Suaeda.* These could have reached the New World via Beringia, probably at different times. Some, like *Artemisia,* have speciated rather heavily in western North America, suggesting that they may have been early immigrants.

The linkage between the Mediterranean region with members of both the Californian and Transmontane botanical regions also seems surprisingly strong considering the distant disjunction involved. Porter (1974) believed that the North American taxa of the zygophyllaceous *Fagonia* may be derived from North African species and that the South American species may have independently reached there from South Africa. Likewise, *Peganum mexicanum* A. Gray, indigenous to the Chihuahuan Desert, may be derived from a North African ancestor although the genus reaches also to central Asia and Mongolia. *Oligomeris linifolia* (Vahl) Macbr., ranging from eastern Mexico across Texas to our southwestern deserts, also occurs in the Mediterranean region. It is the only species of the Resedaceae apparently indigenous in the New World. *Plantago ovata* Forsskal (*P. insularis* Eastw.) and *Senecio flavus* (Decne.) Schultz-Bip. (*S. mohavensis* A. Gray) have a similar distribution. Some of these species may be recent immigrants, having entered with the early Spanish conquistadors. Other southwestern desert genera with strong relationships to the Mediterranean region are *Antirrhinum, Cupressus, Juniperus, Pistachia,* and possibly *Astragalus, Lupinus,* and *Trifolium.* Some of the Arcto-Tertiary elements, like *Acer glabrum* Torr., *Amelanchier utahensis* Koehne, *Fraxinus anomala* Torr. ex S. Wats., *Philadelphus microphyllus* A. Gray, and *Ribes* spp., that have found refuge in the more mesic highlands of the Mojave Desert have more ancient linkage with eastern American and Eurasian representatives.

Thus the flora of the California deserts is of most diverse origin, having been assembled from both adjacent and far-distant sources. Many elements have reached the Southwest by relatively normal overland movement of propagules over long periods of time, propelled no doubt by changing climate. Others may have crossed narrowed straits, seas, or even oceans when sea-level was lowered in glacial epochs, or much earlier

when continents were closer to one another, although later to be forced widely apart by sea-floor spreading and other plate-tectonic movements (Thorne, 1978). Changes in oceanic-current patterns surely were sometimes involved. In other instances, as especially in the amphi-tropical American disjunctions, the only logical explanation has to be long-distance carriage by migratory birds.

This assembling of the Southwestern desert flora has been going on for tens of millions of years, certainly from late Cretaceous to Holocene time. Some of the most distinctive desert taxa, mostly with no close living relatives, could have evolved in Early Tertiary or even Late Cretaceous time. Among them can be listed such endemic western American taxa as the Crossosomataceae, Fouquieriaceae, Garryaceae, Krameriaceae, Lennoaceae, and Simmondsiaceae. It is likely that some of the herbaceous genera that have speciated so heavily in the southwestern deserts to produce the abundant ephemeral annuals have done so in the Holocene, some possibly in the past couple thousand years. Among them are *Astragalus, Camissonia, Chamaesyce, Chorizanthe, Cryptantha, Descurainia, Eriogonum, Gilia, Lupinus, Mimulus, Nemacladus,* and *Phacelia.*

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ANNALS

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VOLUME 73 1986 NUMBER 4

CONTENTS

Seed morphology in North American Campanulaceae *Stanwyn G. Shetler & Nancy R. Morin* 653

Revision of the Guayana Highland Bromeliaceae *Lyman B. Smith* 689

Adiciones a las Leguminosas de la Flora de Nicaragua *Mario Sousa S.* 722

Three New Species of *Solanum* Section *Geminata* (G. Don) Walp. (Solanaceae) from Panama and Western Colombia *Sandra Knapp* 738

A Survey of *Solanum* Prickles and Marsupial Herbivory in Australia *D. E. Symon* 745

Zapoteca: A New Genus of Neotropical Mimosoideae *Héctor M. Hernández* 755

Distribution of Nonprotein Imino and Sulphur Amino Acids in *Zapoteca* *John T. Romeo* 764

A Comparative Study of the Embryology of *Ludwigia* (Onagraceae): Characteristics, Variation, and Relationships *Hiroshi Tobe & Peter H. Raven* 768

Koehneria, a New Genus of Lythraceae from Madagascar *Shirley A. Graham, Hiroshi Tobe & Pieter Baas* 788

Wood Anatomy of Lythraceae—Additional Genera (*Capuronia*, *Galpinia*, *Haitia*, *Orias*, and *Pleurophora*) *Pieter Baas* 810

Contents continued on back cover

VOLUME 73
WINTER 1986
NUMBER 4

ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

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SEED MORPHOLOGY IN NORTH AMERICAN CAMPANULACEAE[1]

STANWYN G. SHETLER[2] AND NANCY R. MORIN[3]

ABSTRACT

Campanulaceae (excluding Lobeliaceae) in North America comprise four genera and 35 species of annual, biennial, and perennial herbs. Generic and specific circumscriptions have been treated variously, and studies of seeds have been few and limited. In this study, seeds of all but one of the native North American species and of selected Eurasian putative relatives were examined with the light and scanning electron microscope. Characteristics of the seeds and their surface cells are described and compared. The seed-coat morphology was found to be relatively uniform, but there are recognizable generic patterns and a number of distinctive individual species. Seeds of *Campanula americana, C. divaricata,* and the other eastern species of *Campanula* are each distinctive and do not show the relative uniformity seen within *Githopsis, Triodanis, Heterocodon,* and the western species of *Campanula.* Seeds of the recently rediscovered *C. robinsiae* and of the wide-ranging *C. aparinoides* are highly distinctive and would appear to set each of these species apart within the genus. However in *Triodanis, T. texana* stands apart. Seeds of *Campanula reverchonii* resemble those of *Triodanis coloradoensis* more than those of other campanulas. Brief speculation on the adaptive significance of seed-coat sculpturing and ornamentation is given.

The Campanulaceae, in the strict sense (excluding Lobeliaceae), are a worldwide family of 35 to 40 genera and perhaps 800 species. Estimates of the number of species have ranged from 600 to 1,000 (Avetisian, 1967; Gadella, 1974; Kovanda, 1978). The species are largely perennial herbs, but some are annuals, biennials, or even small shrubs. The family is confined mainly to north and south temperate regions, being replaced in tropical and subtropical regions by the Lobeliaceae. Only *Wahlenbergia,* with possibly 100 species or more (Thulin, 1975; Carolin, pers. comm., 1981), is well developed in, and in fact restricted to, south temperate regions, especially Australia and South Africa. *Campanula,* the northern counterpart, is the largest genus of the family, comprising some 300 species. It is confined to the north temperate zone, with its center of diversity in Eurasia. Only 23 species occur in North America (Shetler, 1963; Heckard, 1969; Morin, 1980). Three-fourths of these are narrow endemics. Nearly half (11 spp.) of the North American species occurs in the California Floristic Province, and, of these, seven species are endemic there.

The family Campanulaceae is of similar size and diversity in Europe and Soviet Eurasia. *Flora Europaea* (Tutin, editor, 1976) records 13 genera

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and 208 species, *Flora SSSR* (Fedorov, 1957), 19 genera and 223 species. Of these species, the genus *Campanula* accounts for 69% and 67%, respectively. Even allowing for narrower generic concepts, the Russian bellflower flora shows a slightly greater generic diversity. By contrast, the North American Campanulaceae comprise only four genera and 35 species, of which 23, or 65%, belong to *Campanula.* Six (26%) of the latter species are clearly annuals, nearly three times the average percentage of annuals for the genus as a whole. Four of these annual species are found only in California. *Campanula americana* L. has long been considered to be an annual under most circumstances in the wild, but the recent experimental studies of its ecological life cycle by the Baskins (1984) have shown that at least in north-central Kentucky the species behaves as either a winter annual or a biennial.

In the Southern Hemisphere, the family shows limited diversity and is poorly represented except in South Africa, where there are seven, mostly small genera. Two of these, *Cephalostigma* and *Lightfootia,* Thulin (1975) has submerged in *Wahlenbergia.* The latter, with 46 species recognized by Thulin, is the only genus showing substantial diversification in South Africa. It is the only genus of the family found in Australia, where it has radiated at least as much as in South Africa, and in New Zealand, where a few species occur. In South America, where the closely related Lobeliaceae achieve their greatest diversity, the Campanulaceae are represented by only a few species in three genera, including *Wahlenbergia.*

The first and still the only worldwide monograph of Campanulaceae is the one published in 1830 by DeCandolle. He recognized 21 genera and 234 species. Schonland's (1889) systematic conspectus of the family, although badly outdated, is still a standard reference. Generic classification has continued to perplex students of the family, and the question of generic limits continues to draw attention as new lines of evidence are introduced (Avetisian, 1948, 1967, 1973; Charadze, 1949, 1970, 1976; Heidenhain, 1953; Fedorov, 1957; Carolin, 1960, 1967; Contandriopoulos, 1964, 1967, 1970a, 1970b, 1972, 1976; Gadella 1964, 1966; Phitos, 1964, 1965; Damboldt, 1965, 1970, 1975, 1976; Podlech, 1965; Kovanda, 1970a, 1970b, 1977; Dunbar, 1973, 1975a, 1975b; Thulin, 1975; Dunbar & Wallentinus, 1976).

Four genera of Campanulaceae are indigenous to North America: *Campanula* (23 spp.), *Triodanis* (7 spp.), *Githopsis* (4 spp.), and *Heterocodon* (1 sp.). Three of the *Campanula* species have sometimes been placed in other genera. Small (1903) erected the genus *Campanulastrum* for *Campanula americana* (see also Shetler & Matthews, 1967) and the genus *Rotantha* (1933) for *Campanula floridana* S. Wats. ex A. Gray and *C. robinsiae* Small. McVaugh (1945a) placed *C. prenanthoides* Durand in the Eurasian genus *Asyneuma.* Added to the native species are about a dozen exotic species, introduced as ornamentals, that have escaped from cultivation and in some cases (e.g., *Campanula rapunculoides* L.) have become widely naturalized. At least eight species of *Campanula* are well established, as are the following other introduced taxa: *Jasione montana* L., *Legousia speculum-veneris* (L.) Chaix, *Platycodon grandiflorus* (Jacq.) A. DC.,[4] and *Wahlenbergia* cf. *marginata* (Thunberg) DC.

Studies of the seeds of Campanulaceae have been few and limited (Corner, 1976). Seed characters have been little used in the systematics of the group, and a comprehensive study of surface morphology has never been made in this family as a whole. The advent of the scanning electron microscope (SEM) has rejuvenated the whole field of seed morphology (Brisson & Peterson, 1977), however. Among the spate of recent SEM studies are Geslot's (1980) survey of 17 European species of *Campanula* and the two studies dealing with campanulaceous genera by Thulin (1974, 1975), notably his survey (1975) of the seed coats of the species of *Wahlenbergia* in South Africa and Madagascar. Geslot concentrated particularly on *Campanula* subsection *Heterophylla,* examining 11 species of this group. Another important recent contribution is Carolin's (1980) SEM study of seed surfaces in *Goodenia* and related genera of the sister family, Goodeniaceae. Brief reports of our own study also have appeared in print (Morin & Shetler, 1981; Shetler & Morin, 1981).

In our study, we examined the seeds of 38 species of Campanulaceae—32 of the 35 indigenous species and six other species. Seeds could

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[4] The generic name *Platycodon,* compounded from the Greek, is to be treated as a masculine noun (Stafleu, 1978, Art. 74; Stearn, 1966), not a neuter noun, as proposed originally by Alphonse DeCandolle (1830). Accordingly, the correct name for the balloon flower is *P. grandiflorus,* not *P. grandiflorum,* as published by DeCandolle and almost universally followed by others since then.

not be obtained for three of the native species—*Campanula chamissonis* Fedorov (*C. dasyantha* auct.), *C. shetleri* L. Heckard, and *C. wilkinsiana* Greene. The other species examined were: *Asyneuma canescens* (Waldst. & Ket.) Griseb. & Schenck, *A. limonifolia* (L.) Janchen, *Legousia hybrida* (L.) Delarbre, *L. pentagonia* (L.) Druce, *L. speculum-veneris* (L.) Chaix, and *Triodanis falcata* (Ten.) McVaugh. Of the 38 species examined, only 36 are discussed here: *Asyneuma limonifolia* and *Legousia speculum-veneris* are not included.

Together, *Githopsis, Heterocodon,* and *Triodanis* comprise 12 species of indigenous small annuals. *Githopsis,* a genus that has perplexed taxonomists over the years, is found on the west coast of North America from Baja California Norte north to British Columbia. Species of the genus have narrow leaves and clavate capsules that dehisce at the apex by a perforation where the style breaks away. Ewan (1939) reviewed *Githopsis* and recognized seven species. Morin (1983), who revised the genus after studying breeding systems in the group, recognized just four species, including one cleistogamous (autogamous) species with rudimentary flowers, and several subspecies. In the monotypic *Heterocodon,* which also occurs on the west coast from California to British Columbia but extends east to Idaho, Montana, and Nevada, the short, broad capsule dehisces by irregular pores or fissures near the base. Both chasmogamous and cleistogamous flowers are produced regularly, as in *Triodanis.*

Triodanis comprises eight species, seven in North America and one in Eurasia (McVaugh, 1945b; Tutin, 1976). Traditionally they have been included in the genus *Specularia,* now *Legousia.* Tutin (1976), in *Flora Europaea,* retained *T. falcata* in *Legousia.* The genus is characterized by narrowly spiciform inflorescences, tiny cleistogamous early flowers in the lower axils that have vestigial corollas, chasmogamous upper flowers with rotate corollas, and slender, cylindrical or prismatic capsules that open by lateral pores. *Triodanis* can be distinguished from *Legousia* on the basis of the presence of cleistogamous flowers and the relative breadth of the capsules (McVaugh, 1945b, 1948). *Triodanis* species are plants largely of dry open habitats of the plains and canyons of the west and southwest, although *T. perfoliata* (L.) Niewl. and *T. biflora* (R. & P.) Greene (both of which extend into South America) are wide-ranging weeds of disturbed habitats, often growing intermixed. In addition to the seven indigenous species, we also examined the seeds of the Mediterranean *T. falcata.* For comparison, we studied *Legousia hybrida* and *L. speculum-veneris.*

The genus *Campanula* is morphologically heterogeneous. It ranges across North America but is concentrated in the west. It is predominantly a genus of temperate montane, especially subalpine, habitats in North America as well as Eurasia. A few species inhabit truly alpine or arctic habitats. Shetler's (1963) annotated checklist is the only recent synopsis of North American species. He (1982) also has made extensive studies of the Nearctic harebells, the *C. rotundifolia* complex. The four California annual species were treated by Morin (1980), while the annual or biennial *C. americana* has been studied by Shetler (1958, 1962) and Baskin and Baskin (1984). No one has ever produced an infrageneric classification of the American campanulas, and one of the objects of the present study was to examine seed features for evidence of species clusters.

Methods and Materials

Seeds for this study were taken from mature capsules of herbarium specimens on deposit in the herbarium of the University of California, Berkeley (UC), the New York Botanical Garden (NY), and the U.S. National Herbarium (US), Washington, D.C. (Table 1). Measurements were made with an ocular micrometer and stereoscopic microscope. Size of sample per collection, N, was 10 seeds whenever possible, but in some cases only a few seeds were available. Variation was assessed qualitatively by examining seeds from three different populations for each species when possible (Table 1). Seeds were examined under the scanning electron microscope, with as many seeds of a species being mounted on one stub as available or possible. The dried seeds were prepared for SEM study by first rehydrating them with aerosol and then dehydrating them in an alcohol series. From 100% ethanol, the seeds were placed directly into the chamber of a Denton DCP-1 Critical Point Drying Apparatus. After being critical-point dried, the seeds were mounted on SEM stubs with "Elmer's glue" (a water-soluble, animal-based glue) and sputter-coated with carbon and gold-palladium. Sectioned seed coats were obtained by both hand sectioning and spontaneous fracturing. They were examined and photographed in a Cambridge Stereoscan, either the Mark IIA or S410. In a

TABLE 1. List of vouchers of species studied. The "S" numbers are the seed sample numbers, which are used in the figure legends. Unless otherwise indicated, all vouchers are deposited at the U.S. National Herbarium (US).

Asyneuma canescens (Waldst. & Kit.) Griseb. & Schenck
S072, Hungary (?), Transylvania, Olim, *Richter, 12 August 1908*

Asyneuma limonifolium (L.) Janchen
S071, Turkey, Taurus Mts., near Gulek Bogaz ("Gulek-Boghas") pass (= Cilician Gates), *Balansa 627*

Campanula americana L.
S013, Pennsylvania, Allegheny Co., Glenshaw, *Jennings 307a*
S014, North Carolina, Buncombe Co., Craggy Mt., *Biltmore Herbarium 293b*
S015, Canada, Ontario, Amherstburg, *Macoun 54140*
S016, Alabama, Blount Co., near Blountsville, *Kral 37831*

Campanula angustiflora Eastwood
S029, California, Lake Co., Spring Mt., *Morin 249* (UC)
S055, California, Lake Co., Manning Flat, *Bacigalupi & Sweeney 3346* (JEPS)
S056, California, Sonoma Co., Hood Mt., *Baker 11756* (JEPS)
S057, California, Lake Co., Mirabel Mine, *Eastwood & Howell 5530* (JEPS)
S058, California, Santa Cruz Co., Boulder Creek, *Hesse 100a* (JEPS)
S059, California, Santa Cruz Co., Boulder Creek, *Hesse 100b* (JEPS)

Campanula aparinoides Pursh
S060, Minnesota, Clearwater Co., Itasca State Park, *Grant 2848*
S061, New York, Crystal Lake, *McCall, 15 August 1877*
S062, Canada, Quebec, Ile Salaberry (Salaberry de Valleyfield, now Valleyfield), *Rouleau 4256* (UC)
S063, Indiana, Lagrange Co., Adam Lake, *Yuncker & Welch 10717*

Campanula aurita Greene
S086, Alaska, Walker Lake, *Shetler 4962*

Campanula californica (Kell.) Heller
S017, California, Mendocino Co., Point Arena, *Davy & Blasdale 6056*

Campanula divaricata Michaux
S018, Virginia, Augusta Co., Elliott's Knob, *Steele 68*
S019, Kentucky, Whitley Co., Cumberland Falls, *McFarland 49*
S020, Virginia, Page Co., Stony Man Mt., *Lehtonen & Morin, 17 October 1980*

Campanula exigua Rattan
S064, California, Contra Costa Co., Mt. Diablo, *Bowerman 330* (JEPS)

Campanula floridana S. Watson ex A. Gray
S021, Florida, Levy Co., near Cedar Key, *Godfrey 56612*
S022, Florida, Manatee Co., Manatee ("Manitee," now Bradenton), *Garber, April 1876*

Campanula griffinii Morin
S028, California, San Benito Co., Clear Creek, *Griffin 4120* (UC)
S084, California, Napa Co., south of Pope Valley, *Breedlove 5047* (JEPS)
S085, California, Lake Co., Mirabel Mine, *Eastwood 5530* (JEPS)

Campanula lasiocarpa Cham.
S023, Alaska, Aleutian Is., Attu, *Turner 4296*
S024, Canada, Yukon Territory, Mt. Sheldon, *Porsild & Breitung 11731*
S025, Alaska, Cook Inlet, Iliamna Point, *Gorman, 1 September 1902*

Campanula parryi A. Gray
S026, Colorado, Clear Creek Co., Georgetown, *Patterson 97*
S027, Colorado, Archuleta Co., Pagosa Springs, *Wooton 2873*

Campanula piperi Howell
S083, Washington, Clallam Co., Hurricane Ridge, *Shetler 4430*

Campanula prenanthoides Durand
S007, California, Siskiyou Co., Humbug Mt., *Butler 1815*
S008, California, Humboldt Co., Willow Creek, *Tracy 3286*
S009, Oregon, Jackson, Siskiyou Mts., *Heller 13486*

TABLE 1. Continued.

Campanula reverchonii A. Gray
S010, Texas, Burnet Co., Granite Mt., *Palmer 10266*
S011, Texas, Burnet Co., Marble Falls, *Biltmore Herbarium 14893*
S012, Texas *Nealley 149*

Campanula robinsiae Small
S090, Florida, Hernando Co., Chinsegut Hill, *Cooley, Wood & Wilson 6029* (NY)

Campanula rotundifolia L.
S087, Alaska, Kodiak I., *Shetler & Stone 3622*
S088, Colorado, Park Co., near Lake George, *Shetler & Dick 3903*
S089, New York, Tompkins Co., Taughannock Gorge, *Vogelmann 603*

Campanula scabrella Engelm.
S030, California, Siskiyou Co., Mt. Eddy, *Eastwood 2010*
S031, California, Siskiyou Co., Scott Mts., *Engelmann, 30 August 1880* (GH)
S032, Washington, Wenatchie Region, *Brandegee 937* (GH)
S065, California, Siskiyou Co., Mt. Eddy, *Raven 10415* (JEPS)

Campanula scouleri Hook. ex DC.
S005, Washington, Skamania Co., Mt. Prindle, *Suksdorf 11769*
S006, California, Humboldt Co., Rio Dell, *Moldenke & Moldenke 20338*

Campanula sharsmithiae Morin
S066, California, Stanislaus Co., Red Mt., *Sharsmith 3144* (UC)

Campanula uniflora L.
S001, Canada, Baffin I., Frobisher Bay, *Collins 109*
S002, Canada, Quebec, Poste de Payne Bay, *Rousseau 1280*
S003, Canada, Hudson Bay, Belcher Is., *Abbe, Abbe & Marr 4030*
S004, Canada, White I., Frozen Straits, *Angel 37*

Githopsis diffusa A. Gray subsp. *diffusa*
S078, California, Santa Barbara Co., San Roque Canyon, *Pollard, 31 May 1952* (UC)

Githopsis diffusa subsp. *candida* (Ewan) Morin
S079, California, San Diego Co., N of Santa Ysabel, *Munz 9806* (UC)

Githopsis diffusa subsp. *filicaulis* (Ewan) Morin
S082, California, Riverside Co., Sage, *Morin 234* (UC)

Githopsis diffusa subsp. *robusta* Morin
S077, California, Lake Co., Elk Mt., *Koch 960* (UC)

Githopsis pulchella Vatke subsp. *pulchella*
S080, California, Amador Co., Drytown, *Greene, June 1889* (UC)

Githopsis pulchella subsp. *serpentinicola* Morin
S081, California, Tuolumne Co., Yosemite Junction, *Mason 11108* (UC)

Githopsis specularioides Nutt.
S075, California, Humboldt Co., Alder Point, *Tracy 1906* (UC)
S076, California, Shasta Co., near Redding, *Hoover 2279* (UC)

Githopsis tenella Morin
S074, California, Kern Co., Greenhorn Mt., *Morin 241* (UC)

Heterocodon rariflorum Nutt.
S052, California, Marin Co., Mt. Tamalpais, *Herman 17388*
S053, California, Trinity Co., Stuart Fork of Trinity R., *Alexander & Kellogg 5546*
S054, Oregon, Washington Co., Hillsboro, *Howell 1036*; A = chasmogamous flowers, B = cleistogamous flowers

Legousia hybrida (L.) Delarbre
S067, England, Devonshire ("Devon"), ex herb. Hore, 13 July 1826 ("*Prismatocarpus hybridus*")

Legousia pentagonia (L.) Druce
S070, Greece, Aegean Sea, Rhodes (Rodhos) I. ("Isola di Rodi"), *Vaccari 513*

Legousia speculum-veneris (L.) Chaix
S069, Italy, Bay of Naples, Capri I., *Guadagno, May 1905* ("*Specularia hirta*")

TABLE 1. Continued.

Triodanis biflora (R. & P.) Greene
S046, Kansas, Woodson Co., near Yates Center, *Lathrop 545*
S047, Missouri, Baxter, *Bush 15601*; A = chasmogamous flowers, B = cleistogamous flowers
S048, California, Humboldt Co., Klamath R., *Chandler 1415*

Triodanis coloradoensis (Buckley) McVaugh
S033, Texas, Gillespie Co., Crab Apple, *Jermy 468*; cleistogamous flowers sampled ("*Specularia lindheimeri*")
S034, Texas, Kerr Co., Kerrville, *Heller 1731*; A = chasmogamous flowers, B = cleistogamous flowers ("*Specularia lindheimeri*")
S035, Texas, Bexar Co., *Jermy 29* ("*Specularia lindheimeri*")

Triodanis falcata (Ten.) McVaugh
S068, Cyprus, Palaeokhora, *Sintenis & Rigo, 24 September 1880*

Triodanis holzingeri McVaugh
S036, Colorado, Las Animas Co., near Troy, *Rogers 4646*
S037, Arizona, Pima Co., near Sells, *Lehto, Brown, Nash & Pinkava 10738*
S038, Oklahoma, Kiowa Co., near Snyder, *Waterfall 13103*

Triodanis lamprosperma McVaugh
S039, Arkansas, Garland Co., Hot Springs National Park, *Adams, 6 May 1960*

Triodanis leptocarpa (Nutt.) Nieuwl.
S040, Oklahoma, Comanche Co., Mt. Scott, *Waterfall 13075*
S041, Kansas, Woodson Co., *Lathrop 448*
S042, Texas, Tarrant Co., Fort Worth ("Polytechnic"), *Ruth 140*; A = chasmogamous flowers, B = cleistogamous flowers

Triodanis perfoliata (L.) Nieuwl.
S043, Kentucky, Lewis, Big Sulphur Creek, *Braun 4021*
S044, Tennessee, Sevier Co., near Gatlinburg, *Miller 2300*
S045, Maryland, Prince Georges Co., College Park, *McVaugh 1483*

Triodanis texana McVaugh
S049, Texas, Denton Co., Denton, *Whitehouse 15839*; A = chasmogamous flowers, B = cleistogamous flowers
S050, Texas, Dallas Co., Dallas, *Bush 680*
S051, Texas, San Patricio Co., near Aransas Pass, *Whitehouse 18204*

few cases, where shriveling was minimal, the dried seeds were mounted, coated, and examined directly from the herbarium specimens.

Seed coats also were examined and photographed under the light microscope. The seeds were soaked briefly in "aerosol OT," and the coats were teased off, stained with 0.1% Toluidine Blue O, and mounted on a glass side in Hoyer's solution. Camera lucida drawings of these peels were made for many of the species, and a selection of them is included here.

RESULTS

GENERAL DESCRIPTION

The seeds of North American Campanulaceae are generally quite smooth, except in some cases under relatively high magnification (500× or more). Ornamentation of the seed coat is minimal, and only a few species stand out as having noteworthy features. Based on features of seed surfaces, the genera or species-group form relatively homogenous assemblages. In our study, size, shape, and surface pattern tended to be consistent within a given species.

The seeds of all but a few species are elliptical, oblong, or more or less round in outline (Table 2). The cells of the seed coat (testa) usually are fibriform (narrowly fusiform) with thickened, lignified radial walls (Table 3). The surface pattern of the seeds under low magnification is rugose (shallow furrows), reticulate, or striate in most species, depending on the degree of tangential wall collapse (Table 2). When the outer tangential walls have collapsed only slightly, the pattern might be described by Murley's (1951) term *favulariate*, used in her light-microscope studies of crucifer seeds. When these walls have collapsed completely, the seed coat is conspicuously striate or even ribbed (Fig. 26). Tubercles or ridges (enhanced striation) may result from differential thickening of the radial walls (Figs. 35, 38–40,

113, 117). The degree of verrucosity may vary from seed to seed even within the same capsule.

The inner and perhaps the outer tangential walls often are differentially thickened in rings, spirals, or more irregular patterns (Figs. 100, 120, 121). The radial walls also may have thickenings on their inner faces (Figs. 101, 110, 112). The outer or top edges of the radial walls may be smooth or thickened more or less regularly in a pattern of ornamentation that gives the surface of the seed coat a beaded or pebbled appearance (Figs. 35, 38, 39, 113, 117). On the surface, the radial walls may appear to be beaded on the long axis and ridged or upturned at the ends, which gives the surface a wavy or pebbled appearance. In some species there are superficial, noncellular tuberculae or excrescences.

In cross-section, seed shape ranges from terete or oval (Figs. 88–92, 95) to lenticular (Figs. 93, 94, 96, 99) or even triangular (Fig. 97) or quadrangular (Fig. 98; Table 2). Rounded seeds may be flattened asymmetrically toward one rib (Fig. 91). Most of the seeds are truncated at least somewhat at the hilum end and are more or less rounded at the other end. Even in the fusiform seeds, which taper more or less to a point at each end, the hilum end tends to be squared off. In some species, the hilum end is an organized, well-marked, symmetrical region (e.g., *Campanula americana,* Fig. 94), while in many other species this end is little more than an asymmetrical slit or pinched-off zone (Figs. 88–93).

The radial walls of testa cells may be thin and the lumen large and open (Figs. 102, 103), or thick and the lumen narrow and slit-like (Figs. 109, 111) or hour-glass-shaped in cross-section, as when the radial walls are rod-like (Figs. 106, 107, 112). In some cases (not depicted), the lumen appears to be widest in the middle and the radial walls somewhat hour-glass-shaped. Some species have pitted radial walls (Figs. 102–104, 120c), and at least one species, *C. floridana* (Fig. 105), has large, irregularly shaped foramina in the walls. Seed coats with cells that have thin radial walls and large lumina tend to have cells that are almost isodiametric in surface view and are deeper than long or wide (Figs. 102, 103, 120c). The area where the cells meet appears either as a trough or a ridge in some species, but in other species it can be observed only with difficulty if at all (cf. e.g., Figs. 14, 66, 108). The surface of the seed coat may have a relatively thick layer of non-cellular material or virtually none (cf. Figs. 44, 100–112). A distinct cuticle is detectable in some species, as in *Triodanis texana* (Fig. 116).

The seed-coat cells of North American Campanulaceae can be divided into the three basic types described below. Cell type is indicated in Table 3 for every species studied.

Type 1. Cells elongate, fusiform or fibriform, with relatively thick radial walls and narrow, often indistinct lumen. The cells form a continuous weave without clearly squared, abutting end-walls and often without clear indication of where one cell ends and another begins (e.g., *Campanula griffinii,* Figs. 4, 120a).

Type 2. Cells trapezoidal or irregularly hexagonal with thick to moderately thick radial walls and narrow to relatively wide lumen. The cells form a distinct reticulum with obvious cell outlines and cell ends, even when the outer tangential walls have not collapsed. When the tangential walls collapse, the surface appears ribbed (e.g., *C. divaricata,* Figs. 34, 120b).

Type 3. Cells more or less isodiametric in face view, hexagonal or lobed, with large deep lumen and relatively thin radial walls having pits or foramina. The cells form a jigsaw-puzzle or quilted pattern (e.g., *C. aparinoides,* Figs. 31, 102, 120c).

Campanula

The mature seeds range in length from 0.4 mm to 1.6 mm and in width from 0.2 mm to 0.9 mm, with the length/width ratio ranging from 1.0 to 3.3 (Table 2). The color ranges from buff to rich chestnut brown. The surface pattern is more or less reticulate (often appearing striate), the degree depending on the thickness of the radial walls, relative dimensions of the cells, and the extent of the tangential-wall collapse. The wider the cells, thinner the radial walls, and more collapsed the outer tangential walls, the more reticulate the surface pattern. The individual cells are the units of the reticulum. The narrower the cells, thicker the radial walls, and the more intact the outer tangential walls, the less reticulate and more striate or rugose the seed coat appears.

The Cordilleran campanulas, *C. scabrella* (Figs. 9, 10), *C. parryi* (Figs. 11, 12), *C. piperi* (Figs. 13, 14), and *C. aurita* (Figs. 15, 16), form a relatively homogeneous group based on seed characteristics. The widest-ranging of these, *C. parryi,* has the smallest seeds—0.5–0.6 mm long—distinguishing it from the larger-seeded (0.7–1.0 mm) *C. scabrella,* with which it sometimes is confused (Table 2). Closely similar are *C. uni-*

TABLE 2. Comparison of seed shape, size, surface, and presence and placement of wings of seeds of North American Campanulaceae and possible relatives.

Taxon	Shape		Approx. Length[1] L/W (mm)		Surface	Wings[2]
	Longitudinal	Cross-section				
Asyneuma						
canescens	long-ovate	ovate	1.6	2.2	shallow furrows	)
Campanula						
americana	oblong	lenticular	1.3–1.6	1.5–1.7	pebbled	( )
angustiflora	ovate	broadly ovate	0.7	2	faintly striate	)
aparinoides	oblong	terete to triangular	0.7	1.3–2.3	shallowly colliculate	—
aurita	oblong	narrowly ovate	1.2	2	interrupted striate	( )
californica	elliptical to obovate	broadly ovate	0.9	1.7	interrupted striate	—
divaricata	oblong	terete	0.7	2	reticulate	)
exigua	oblong	ovate	0.7	2	faintly striate	)
floridana	broadly elliptical to quadrangular	terete ovate	0.6	1.5	rugose	)
griffinii	oblong	ovate	0.6–1.1	2.2	faintly striate	)
lasiocarpa	fusiform to ovate	terete	0.7	2	striate	—
parryi	elliptical	terete	0.6	1.8	striate	V
piperi	narrowly elliptical	terete	0.7	2	striate	^ V
prenanthoides	oblong	ovate-flattened	0.9	2.2	striate	)
reverchonii	broadly elliptical-roundish	lenticular	0.9	1.3	striate	—
robinsiae	roundish	triangular	0.4	1	margins tuberculate	—
rotundifolia	oblong	terete to ovate	0.8	2	striate	)
scabrella	oblong	ovate	0.7–1.0	1.5–3.3	striate	)
scouleri	oblong	ovate	1.0	2	striate-reticulate	)
sharsmithiae	oblong	terete	0.8	2.6	smooth	—
uniflora	oblong	terete	1.0	2	striate	)
Githopsis						
diffusa	fusiform	terete	0.6–0.8	3.0–3.8	striate	)
pulchella	fusiform	terete	0.7–1.0	2.4	striate	)
specularioides	fusiform	terete	0.8	2.6	striate	)
tenella	fusiform	terete	0.7	1.8	flattened reticulum	)
Heterocodon						
rariflorum	elliptical	terete	0.5	1.7–2.1	smooth	^
Legousia						
hybrida	elliptical	terete	1.4	1.6	shallow furrows	—
pentagonia	elliptical	narrowly elliptical	1.5	1.6	shallow furrows	—
Triodanis						
biflora	broadly elliptical	lenticular	0.5	1.3	shallow furrows	( )
coloradoensis	broadly elliptical	lenticular	0.8	1.4	shallow furrows	( )
falcata	broadly elliptical	lenticular	0.8	1.4	shallow furrows	( )
holzingeri	broadly elliptical	lenticular	0.5	1.5	scattered tubercles	( )
lamprosperma	broadly elliptical to roundish	lenticular	0.9	1.2	shallow furrows	( )

TABLE 2. Continued.

Taxon	Shape		Approx. Length[1] L/W (mm)		Surface	Wings[2]
	Longitudinal	Cross-section				
leptocarpa	broadly elliptical to ovate	lenticular	0.8	1.6	shallow furrows	( )
perfoliata	broadly elliptical to roundish	lenticular	0.5	1.3	smooth or tuberculate	( )
texana	broadly elliptical	quadrangular	0.4	1.4		( )

[1] See text for ranges. Approximate range given here only for exceptionally variable species.
[2]) = peripheral ridge on one side only; ( ) = ridge essentially on entire periphery; ∧ = ridge on hilum end; ∨ = ridge on end opposite hilum.

flora (Figs. 17, 18), *C. rotundifolia* (Figs. 19, 20), and *C. lasiocarpa* (Figs. 21, 22). These seven compose what might be regarded as the most common or typical campanula seed type in North America. The cellular pattern is Type 1 with gradation to Type 2.

The California annuals, *Campanula angustiflora, C. exigua, C. griffinii,* and *C. sharsmithiae* (Figs. 1–8, 93), have seeds that are extremely smooth, almost featureless, except under high magnification, and even at 500× the surface may be flat and smooth, as *C. sharsmithiae* (Fig. 8). The latter species, only recently discovered (Morin, 1980), is a narrow serpentine endemic of the Mt. Hamilton endemic area of California. Its cucumber-shaped seeds tend to be larger, smoother, and more nearly terete than the seeds of the other three annual species. The four species have the Type 1 cellular pattern.

Campanula prenanthoides (Figs. 23, 24) and *C. scouleri* (Figs. 25–27), also west coast species, share a similar seed-coat morphology with a Type 2, or Type 1 grading to Type 2, pattern, and they stand somewhat by themselves. The seeds of *C. scouleri* are large, about 1 mm long and 0.5 mm wide. The surface pattern is reticulate and ribbed when the outer tangential walls are collapsed (Fig. 26), but quite smooth when they have not collapsed (Fig. 27). The *C. prenanthoides* seed is distinctive in cross-section, being round on one side and compressed to a margin or flange on the other side (Fig. 91). The seeds of *Asyneuma canescens* (Figs. 28, 29) are similar to those of *C. prenanthoides* and *C. scouleri* in shape and outline. In addition, all three species have thick-walled, fibriform cells.

The three marsh species of North America, *C. aparinoides, C. floridana,* and *C. californica,* have distinctive seeds. The seeds of *C. californica* are generally similar to those of *C. prenanthoides* and *C. scouleri. Campanula californica* (Figs. 32, 33) also has large seeds (0.9 mm long) with a shape similar to these species, but these are less conspicuously biconvex and have more typically a Type 1 surface pattern. The surface cells are quite deep (Fig. 109), however, possibly resulting in enhanced bouyancy.

The seed coat of *C. aparinoides* (Figs. 30, 31, 120c) is unlike any other in the genus. The cells are Type 3, essentially isodiametric in surface view, resembling tiny "oyster crackers" that fit together in a quilted pattern. The individual cells (Figs. 102, 103) have a large deep lumen and thin radial walls that have small pits visible under high magnification (2,000×). In recent studies of the *C. aparinoides-C. uliginosa* complex, Cochrane (1981; pers. comm.) has found seed differences and other taxonomic characters that, in her opinion, justify treating the two as distinct subspecies of *C. aparinoides,* instead of lumping them as a single taxon, as is now customary.

The seeds of *C. floridana* (Figs. 36, 37) are small (0.6 mm long) with a rugose surface pattern. The cells of the seed coat are trapezoidal or roughly hexagonal with a large lumen and can be classed as Type 2 (Fig. 121e). The seeds are more or less terete in cross-section (Fig. 89) and have radial walls that are thin and have large, irregular openings that impart a "Swiss cheese" appearance (Fig. 105).

In seed-coat pattern, *C. divaricata* (Figs. 34, 35, 120b), the Appalachian bellflower, shows no clear affinity to any other species, although it approaches the pattern in *C. floridana.* The seed coat is reticulate with trapezoidal or hexagonal cells that perhaps best exemplify Type 2. The radial walls are moderately thick to thin and the lumen is large. The most distinctive feature is

TABLE 3. Comparison of surface seed-coat cells.

Taxon	Type	Shape	Lumen	Wall Thickness
Asyneuma	2	fibriform 80 × 10 μm	narrow	thick
Campanula				
americana	1	fibriform 72 × 11 μm	narrow	thick
angustiflora	1	oblong 43 × 10 μm	medium	variable
aparinoides	3	isodiametric 30 × 19 μm	large	thin
aurita	1–2	oblong	narrow	thick
californica	1	oblong 52 × 8.6 μm	medium	medium
divaricata	2	broad-fibriform 71 × 18 μm	large	thin
exigua	1	broad-fibriform 42 × 4.5 μm	narrow	thick
floridana	2–3	isodiametric 62 × 29 μm	large	thin
griffini	1	fibriform 66 × 10 μm	narrow	thick
lasiocarpa	1–2	fibriform 94 × 10 μm	narrow	thick
parryi	1	broad-fibriform 50 × 9 μm	medium	thick
piperi	1	broad-fibriform 60 × 7 μm	narrow	thick
prenanthoides	2	fibriform 60 × 7 μm	medium	thick
reverchonii	1	fibriform 54 × 7 μm	narrow	medium
robinsiae	3	isodiametric	cell structure not visible unknown in peels	
rotundifolia	1–2	fibriform 70 × 10 μm	medium	thick
scabrella	1–2	fibriform 56 × 14 μm	medium	medium
scouleri	1–2	fibriform 72 × 7 μm	narrow	thick
sharsmithiae	1	irregular 52 × 11 μm	medium	thick
uniflora	1–2	fibriform 59 × 11 μm	narrow	thick
Githopsis				
diffusa	1–2	long-fibriform 109 × 6.9 μm	medium	thin
pulchella	1–2	fibriform 79 × 10 μm	broad	medium
specularioides	1	fibriform 89 × 8 μm	medium	medium
tenella	2	short-fibriform 49 × 9 μm	broad	medium
Heterocodon				
rariflorum	1	fibriform 62 × 8.4 μm	narrow	thick

TABLE 3. Continued.

Taxon	Type	Shape	Lumen	Wall Thickness
Legousia				
hybrida	1	fibriform 74 × 9.2 μm	medium	thick
Triodanis				
biflora	1	fibriform 96 × 6.4 μm	narrow	thick
coloradoensis	1	fibriform 51 × 8.6 μm	wide	medium
falcata	2	fibriform 55 × 9.2 μm	narrow	thick
holzingeri	1	fibriform 60 × 10 μm	narrow	thick
lamprosperma	1	fibriform 75 × 9 μm	narrow	medium
leptocarpa	1	fibriform 150 × 9.4 μm	narrow	thick
perfoliata	1	fibriform 71 × 8.85 μm	narrow	thick
texana	2–3	short-fusiform 54 × 15 μm	narrow	medium

the regularly beaded outer edge of the radial walls (Figs. 35, 113).

The three non-Californian annual, winter-annual, or biennial species—*C. americana, C. reverchonii,* and *C. robinsiae*—have their own distinct seed-coat patterns. The seeds of *Campanula americana* (Figs. 38–40, 94, 121a), a wide-ranging species of woodland borders in eastern North America, have fibriform cells with thick radial walls and a narrow lumen. The radial walls have dense spirals of apparent secondary thickenings. The end walls are thickened into ridges that give the surface a pebbled or verrucose ornamentation under a thick cuticle (Figs. 39, 40). The seed is lenticular in cross-section (Fig. 94) and has a definite winged margin or flange the whole way around. The hilum end is truncated, more organized than in other species, and outlined by the heavy, symmetrical flange as an oval area.

Campanula robinsiae (Figs. 41–44, 97, 118) has the smallest seeds recorded for the North American members of the genus (Table 2). The surface is very smooth, and the seed is trigonous in cross-section; the angles are distinctly ridged and each has irregularly placed, smoothly rounded tubercles along it (Fig. 97). The seed-coat cells (Fig. 118) are of Type 3, digitate or lobed, with the lobes interlocking with other cells like the pieces of a jigsaw puzzle.

Campanula reverchonii (Figs. 67, 68, 96), the basin bellflower of the Edwards Plateau of Texas, has seeds that are quite similar to the seeds of *Triodanis* species. The seed is elliptical in outline and more or less lenticular in cross-section (Fig. 96). The seed coat has Type 1 cells with a rugose or striate appearance.

HETEROCODON

Heterocodon rariflorum (Figs. 84, 85) has small (0.5–0.6 mm long) elliptical seeds that are terete in cross-section. The surface is very finely striate, being composed of long, narrow cells of Type 1.

TRIODANIS

Triodanis seeds are lenticular to elliptical in outline and lenticular (biconvex) in cross-section (Fig. 99). Excepting *T. texana* (Figs. 54–56), the seed coats have Type 1 cells, and the surfaces appear rugose, striate, or smooth. *Triodanis perfoliata* (Figs. 45–48, 104, 119), *T. holzingeri* (Figs. 49, 50, 99), *T. biflora* (Figs. 51–53, 112), and *T. texana* (Figs. 54–56, 98) have seeds that are 0.4–0.6 mm long. *Triodanis coloradoensis* (Figs. 57, 58), and *T. lamprosperma* (Figs. 61, 62), as well as the European *T. falcata* (Figs. 59, 60), have seeds that are 0.8–0.9 mm long. The seeds of *T. leptocarpa* (Figs. 63–66), which are more elongate, are about 0.8 mm long. *Triodanis falcata,* the European species, apart from a somewhat

smoother seed coat, fits right into the seed pattern of this largely North American genus. The radial walls of *Triodanis* are thick and rodlike (Fig. 112) and may have pits (Fig. 104). The surface may be verrucose or pebbled (Fig. 119) from irregular thickenings. In *T. perfoliata,* some populations have smooth seeds, while other populations have seed coats that are finely tuberculate with the tubercles in lines (cf. Figs. 45–48). McVaugh (1945b) studied this variation quantitatively with the light microscope.

Triodanis texana (Figs. 54–56, 98, 121b) clearly stands alone, not just within the genus but in the North American Campanulaceae generally. In outline, the seed is similar in shape to other seeds of *Triodanis,* but in cross-section (Fig. 98) it is quadrangular rather than lenticular. The cell type is intermediate between 2 and 3, although many cells are almost isodiametric, if irregularly so. The outer cell surfaces, presumably the tangential walls, are strongly convex and covered by a definite cuticle, which can be seen peeling away intact in Figure 116. The cells form a braided surface pattern like the surface of a cord or rope with its interwoven strands.

Seeds of cleistogamous and chasmogamous flowers were examined in *T. leptocarpa* (Figs. 63–66) and *T. texana,* but no consistent differences were observed in seed-coat morphology between seeds of the chasmogamous and cleistogamous flowers.

GITHOPSIS

The mature seeds of *Githopsis* (Figs. 69–81, 110, 115) range in length from 0.6 to 1.0 mm and in width from 0.2 to 0.4 mm, with the length/width ratio ranging from 1.8 to 3.8 (Table 2). The seeds are fusiform, more or less tapering to both ends and are terete in cross-section (Fig. 92). The surface pattern is fibriform-rugose to fibriform-reticulate in *G. pulchella* (Figs. 76–79, 115). The pattern appears striate in low magnification owing to the longitudinal ridges of the radial walls and the troughs of the lumina (Fig. 115). The cells are Type 1, grading to Type 2 particularly in *G. pulchella* (Table 3). *Githopsis tenella* (Figs. 74, 75) has the most fibriform pattern with the smoothest surface, owing to the very narrow lumina. The subspecies of *G. diffusa* (Figs. 69–73) are all similar in their surface patterns, as are the subspecies of *G. pulchella* (Figs. 76–79). The radial walls are thick and rod-like—ropy in surface view. In general, they are wider than the almost slit-like lumina, although the width of the lumen is variable in *G. diffusa* and relatively large in *G. pulchella.*

The seeds of the four species of *Githopsis* and their subspecies, as recognized by Morin (1983), are distinguishable primarily on the basis of size. *Githopsis tenella* seeds are the most distinctive of the four species because of the density and small size of the seed-coat cells.

DISCUSSION

Seed-coat morphology in the North American Campanulaceae is relatively uniform, but there are recognizable generic patterns and a number of distinctive patterns in individual species. *Githopsis* seeds, although clearly similar to seeds of the majority of *Campanula* species, stand together with their fusiform shape and similar surface patterns of cells that have thick, rounded radial walls that look inflated, almost sausage-like. Individual cells of the testa look like miniature inflatable rafts (Fig. 115).

The more or less lenticular seed with Type 1 cells and a fibriform surface pattern is consistent within *Triodanis,* although the seeds of *T. leptocarpa* (Figs. 63, 65) are more elongate and oval than in the other species. Mediterranean *Triodanis falcata* (Figs. 59, 60), which in *Flora Europaea* (Tutin, 1976) is treated as a species of *Legousia,* fits in well with the larger-seeded American *Triodanis* species, although in cross-section the seeds are more rounded than typical *Triodanis* seeds. The one species that does not conform, except in the oval outline, is *T. texana* (Figs. 54–56, 98, 116). Its quadrangular seeds with an undulating surface pattern have no counterpart either in the genus or the family in North America. The seed-coat cells are irregular, thick-walled sclereids (Fig. 121b).

Triodanis often is included in *Legousia* (*Specularia*). Indeed, the seeds of *Legousia pentagonia* (Figs. 86, 87) and *L. speculum-veneris* (not shown) are similar in shape (outline and cross-section), especially to the seeds of the large-seeded *Triodanis* species (Figs. 57–66). The large seeds of *Legousia hybrida*—largest of the seeds studied—are rounded rather than lenticular in cross-section, and the cells of the testa are quite different from those of *Triodanis* (cf. Figs. 111, 112). These two genera clearly cannot be separated easily on the basis of their seeds, although more study particularly of *Legousia* species is needed.

The seeds of *Campanula reverchonii* (Figs. 67,

96) show definite similarities to the seeds of *Triodanis*. *Campanula reverchonii* is endemic to the granitic Central Basin or Llano Area of the Edwards Plateau in central Texas (Correll & Johnston, 1970). All American species of *Triodanis* are found in Texas; two of the seven species, *T. coloradoensis* and *T. texana*, are endemic to Texas, the former to the Edwards Plateau. Further study is needed of the relationships of *Triodanis* to *C. reverchonii*, which is not unlike some *Triodanis* species in habit. The seed similarity may be the result of convergence through environmental selection.

The relationship of *Heterocodon* to other genera is uncertain. McVaugh transferred it to *Specularia* in 1941 but subsequently (1945b) divided this latter genus into *Triodanis* and *Specularia* (*Legousia*) and reinstated the genus *Heterocodon*. In this later paper McVaugh suggested that he was maintaining it as separate from *Campanula* primarily because of tradition. The seeds of *Heterocodon*, although at the other end of the size range, are more similar to those of *L. hybrida* than to those of the other two species of *Legousia* examined or to any of the other taxa studied by us. The similarity of *Heterocodon* seeds to *Legousia* seeds and the fact that *Heterocodon* and *Triodanis* regularly produce cleistogamous as well as chasmogamous flowers support the theory that *Heterocodon* belongs in the *Legousia-Triodanis* complex.

Within *Campanula*, some weak groupings can be made, but for the most part the individual exceptions are more notable than the common patterns. The California annuals form a small group of four species. However, the seed of *C. sharsmithiae* (Figs. 7, 8) has a more terete shape and a smoother surface than the other three, owing, apparently, to a thicker cuticular layer.

The position of *Campanula californica* in the genus is uncertain. On the basis of seed morphology, it does not belong with the other two species of marshes, swamps, and bogs—*C. aparinoides* and *C. floridana*. The seeds suggest that its affinities might be much closer to *C. scouleri* and perhaps *C. prenanthoides*. McVaugh (1945a) transferred *C. prenanthoides* to the Eurasian genus *Asyneuma* because of its deeply lobed corolla. The similarity between the seeds of *A. canescens*, *C. prenanthoides*, *C. scouleri*, and *C. californica* suggests to us that these species may be related to each other.

The western American perennial alpine species of *Campanula* have a more or less common seed pattern, although with variation. Although they differ markedly in size, the seeds of *C. aurita* and *C. parryi* have a very similar surface pattern. These species have other morphological similarities and to some extent are ecological counterparts, with *C. aurita* occurring in the far northern Rocky Mountains (Brooks Range) and Yukon Tablelands and *C. parryi* occurring in the central and southern Rockies. The two Pacific Northwest species, *C. piperi* and *C. scabrella*, ecological counterparts in the Olympic Mountains and Cascade Mountains, respectively, have quite similar seed-coat patterns (Figs. 10, 14, 121c), which also are generally like the patterns of *C. aurita* and *C. parryi* (Figs. 12, 16, 121d). The Olympic Mountain bellflower, a local endemic, resembles a smaller version of *C. aurita*, but there also are morphological grounds for regarding it as closely related to the downy alpine bellflower (*C. scabrella*). The latter forms almost a morphological continuum with *C. parryi* in the Northwest, although seed size seems to be a reliable character for distinguishing between the species.

On the basis of the seeds, *Campanula uniflora* (Figs. 17, 18), which otherwise appears to have no close relatives, does not stand apart noticeably from the other perennial bellflowers of western North America.

In eastern North America, *Campanula* is heterogeneous with respect to seed-coat pattern. Each species stands more or less alone, although *C. divaricata* and *C. floridana* have the same type of epidermal cell pattern (Figs. 34–37, 120b, 121e). It is possible that these two species have been derived from a common ancestor, but this possibility has never been raised before. Both, but particularly *C. divaricata*, show some similarity in cell pattern to the more northern and wide-ranging *C. rotundifolia* (Figs. 19, 20, 108, 114). The distinctive beaded thickenings on the radial walls of *C. divaricata* (Figs. 35, 113) are encountered sometimes also in the western *C. parryi* (Fig. 117), but on general morphological grounds these two species appear to be unrelated.

Like the tall bellflower, *Campanula aparinoides* and *C. robinsiae* each stand apart from other taxa in the genus in North America. *Campanula aparinoides* does not appear to be closely related to *C. floridana* (Cochrane, pers. comm.), contrary to Shetler's (1963) earlier speculation on the basis of ecology and general morphology. The two have altogether different seed types (Figs. 30, 31, 36, 37, 89, 95, 120c, 121e), including

quite different epidermal cells, although in both species these cells are relatively thin-walled with large lumina and pitted or fenestrate radial walls (Figs. 102, 103, 105; see also Cochrane, 1981). Small (1926) initially considered *C. robinsiae* to be most closely related to *C. reverchonii* but later (1933) placed it, with *C. floridana,* in his genus *Rotantha* (Figs. 41–44, 67, 68, 96, 97). The seeds of these three species bear little resemblance to each other and certainly would not support this view.

Of all North American Campanulaceae, *C. robinsiae* has the most unusual and distinctive seeds. This raises new questions about the origin of this elusive species, thought possibly to be extinct until its recent rediscovery. It is a small annual of puzzling origin (Shetler, 1963), known only from its type locality at Chinsegut Hill, near Brooksville, Florida. It had not been seen in the wild since 1958 until the spring of 1983 when it was found in several vernal pools in the Chinsegut Hill area first by Steven Hill and subsequently by others, including the authors. Surprisingly, it was not mentioned in Ward's recent book (1979) on rare and endangered plants of Florida, presumably because it was thought to be extinct or of doubtful origin in the first place. As an annual, this species may go through cycles of abundance and sparsity, and, being so small and inconspicuous, it is easily overlooked even when fully developed. The unusual seed morphology deepens the mystery of this plant's affinities. If there is any justification for Small's genus *Rotantha,* it is the suite of characters that seems to isolate *C. robinsiae* from the other species. Further studies are being conducted by the authors in collaboration with Steven Hill.

The affinities of *C. americana,* the tall bellflower, also remain obscure. This highly distinctive species with dense spicate racemes of star-shaped, rotate flowers; tall, often much-branched stems; and annual or biennial habit was given its own genus, *Campanulastrum,* by Small in 1903. Although the basic floral morphology is campanuloid, it does not fit well into the typical concept of *Campanula.* Small's view appears to have increasing justification from palynological, cytological, and now seed evidence. The pollen grains are pantaporate, a condition unique to only a few species among many species with 3–4-porate grains in *Campanula* (Avetisian, 1967). Chromosome number is $n = 29$, unique in the genus largely comprising species in the $n = 17$-series (Gadella, 1964). Surely this is a derived number, probably through hybridization. Seed-coat morphology also is unique. The upturned ends of the radial walls, which seem to be responsible largely for the pebbled surface, occur to a limited extent in *C. parryi* (Figs. 38–40, 117), but on other grounds these species do not appear to be related. The isolated position of *C. americana,* further underscored by Gadella's (1964) inability to cross it with other campanulas, led Shetler (Shetler & Mathews, 1967) some time ago to support its placement in the genus *Campanulastrum.* Gadella, puzzled by *C. americana,* suggested that a search should be made among species of *Asyneuma,* which also have deeply cut corollas, for the origins or relationships of *C. americana.* Interestingly, the seeds of *A. canescens* (Figs. 28, 29) and *C. americana* (Figs. 38–40, 121a) appear to have similar epidermal cell patterns beneath their cuticular layers.

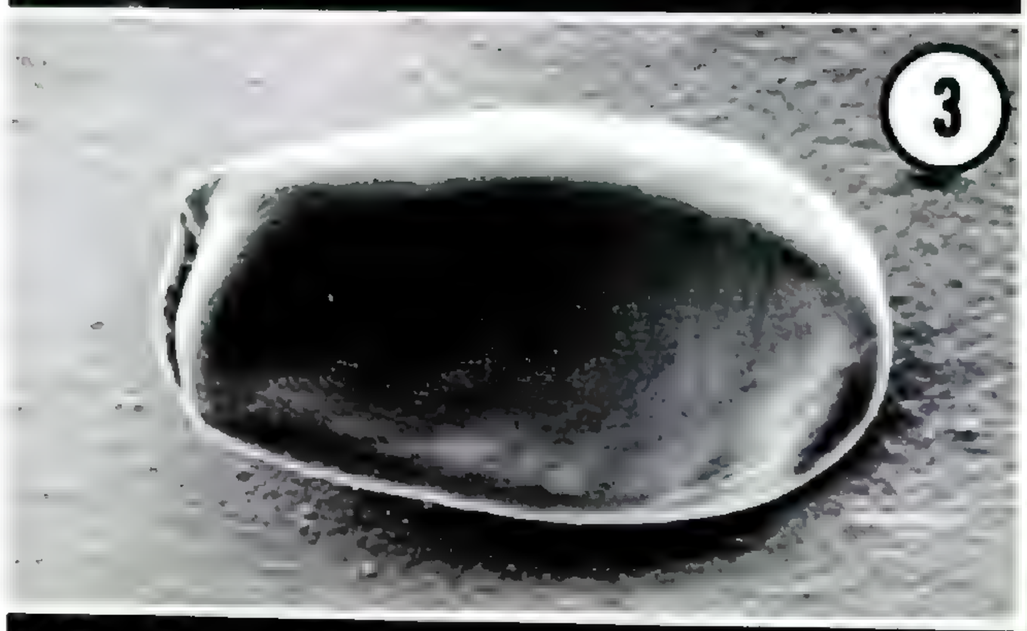
The adaptive significance of seed-coat sculpturing and ornamentation has been little studied. The seeds of bellflowers (Campanulaceae) apparently are dispersed mainly by water, with gravity playing an important role among those species that grow on rock ledges and cliff faces (e.g., *C. rotundifolia*). The relatively smooth, rounded seeds seem to be streamlined to facilitate water dispersal, and the seeds have no obvious adaptations for animal or bird dispersal. They are small and insignificant as a source of food, and, with the exception of *Campanula robinsiae* (Figs. 41–44) and *Triodanis perfoliata* (Figs. 45–48), lack superficial processes or ornamentation that might enhance their chances of being carried by animals. In the case of these two species, the tubercles are so minute that it is doubtful they have any dispersal role with respect to animals. Possibly, ants play a role in the dispersal of some or all bellflowers, and one can hypothesize that such tiny processes as these might facilitate transporting the seeds when ants are the dispersal agents. *Triodanis perfoliata* is wide-ranging, and perhaps tubercles confer a selective advantage in dispersal at least in some environments. This species is variable with respect to seed-coat tubercles, and the ratio of tuberculate to non-tuberculate seeds varies not only from population to population but also from region to region (McVaugh, 1945b). What selective advantage, if any, is conferred by the tubercles or lack of them, is not known.

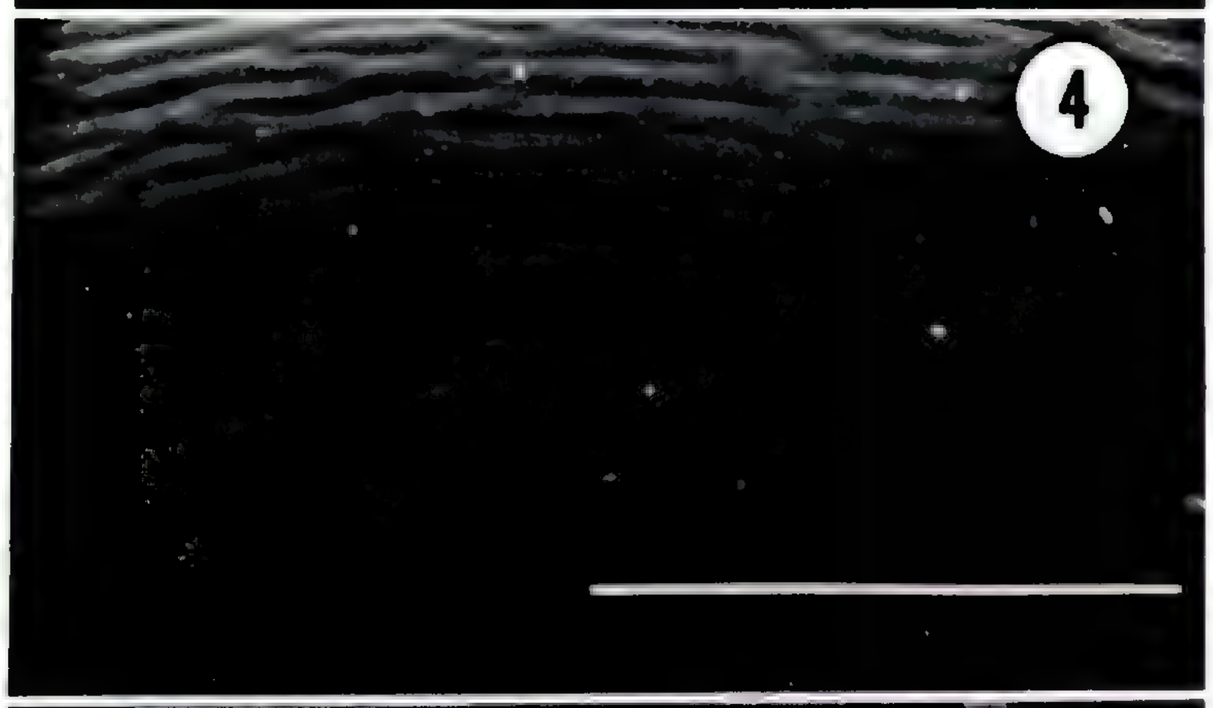
Two of the marsh/swamp species, *Campanula aparinoides* and *C. floridana,* have epidermal cells with relatively large lumina and thin walls that

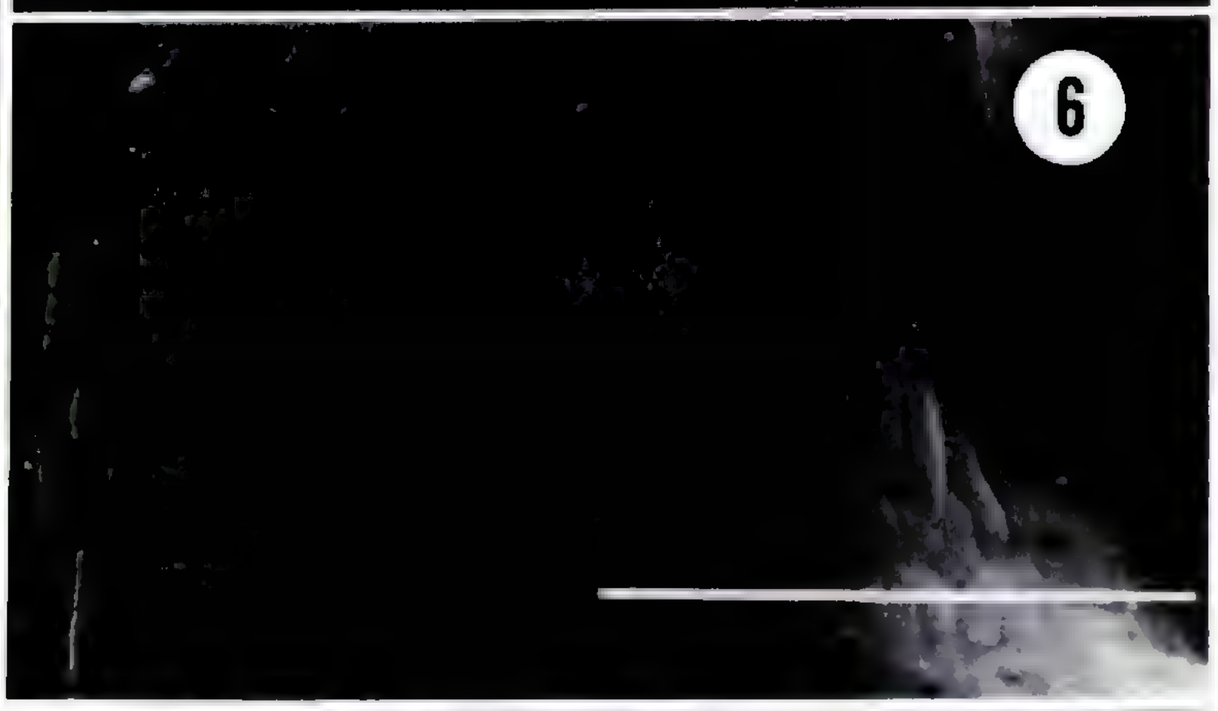
have many pits or, in the case of *C. floridana,* large foramina (Figs. 102, 103, 105). Perhaps these cell characteristics give the seeds of these two species greater buoyancy in the hydric environment. At the same time, pits are not restricted to these species (cf. *Triodanis perfoliata,* Fig. 104).

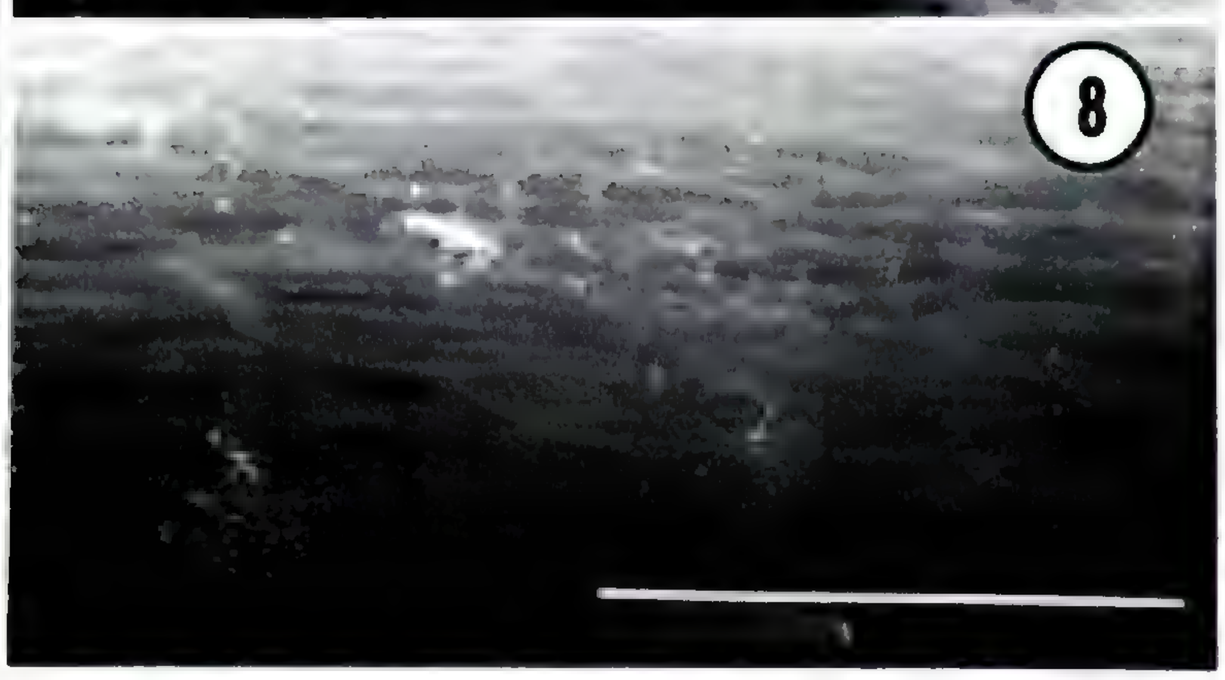
The seeds of the annual species have a "tight weave" of fibriform cells with thick radial walls that nearly fill the lumina and have a definite cuticle or layer of relatively smooth, non-cellular material on the outside of the testa. Perhaps such features have selective advantages in dry or disturbed habitats in preventing easy water-loss or water-logging by the seeds (Figs. 1–8, 38–40, 45–87).

Little is known about general trends of evolutionary specialization in seed-coat sculpturing, and the relatively few species of bellflowers in North America do not provide an adequate basis in themselves for reliable speculation about seed-coat phylogeny in the Campanulaceae. If there is a typical seed coat in North America, it would appear to be the type found among the western American perennial species. The annuals of the genus *Campanula* and of the family at large in North America, as well as the perennials in eastern North America (except *C. rotundifolia*) appear to represent several different tendencies in specialization of the seed coat. It is not clear whether these tendencies have evolved in North America in response to ecological or other selective factors, or represent tendencies to be found elsewhere in the family in Eurasia or perhaps even in the southern hemisphere in *Wahlenbergia.* Thulin's (1975) study of South African *Wahlenbergia* species shows some intriguing similarities in seed-coat sculpturing and seed shape. For instance, the pictured seed of *W. virgata* is very much like *Githopsis* seeds, and the seed of *W. subaphylla* resembles those of *Campanula prenanthoides.* Clearly, more study of the family worldwide is needed before the results presented here can be fully interpreted.

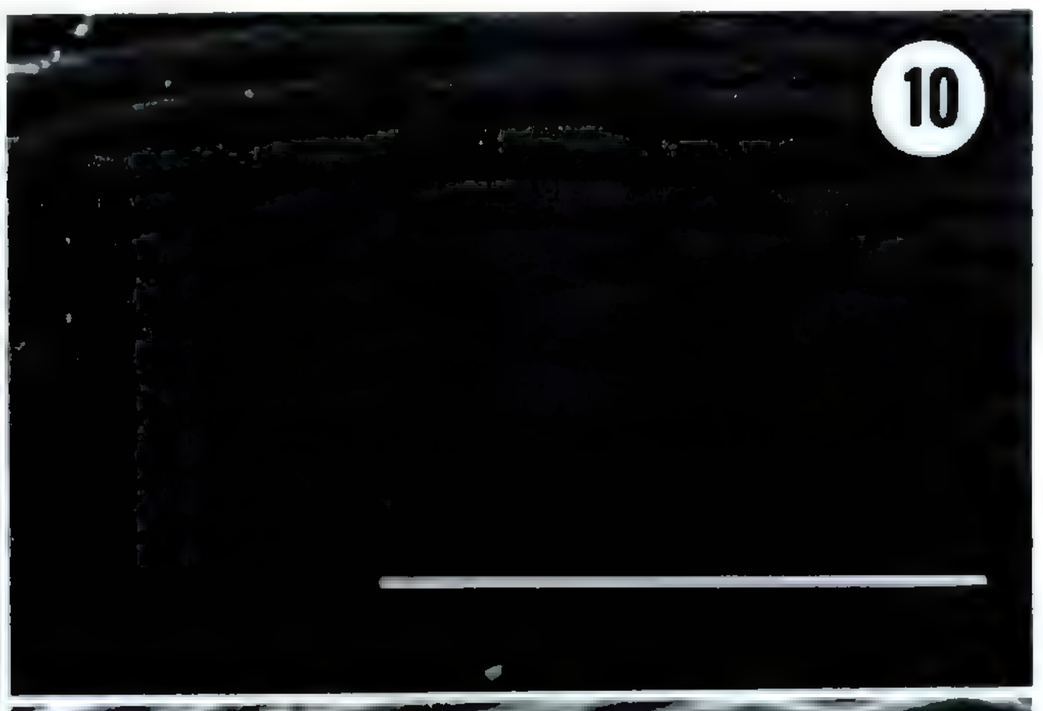


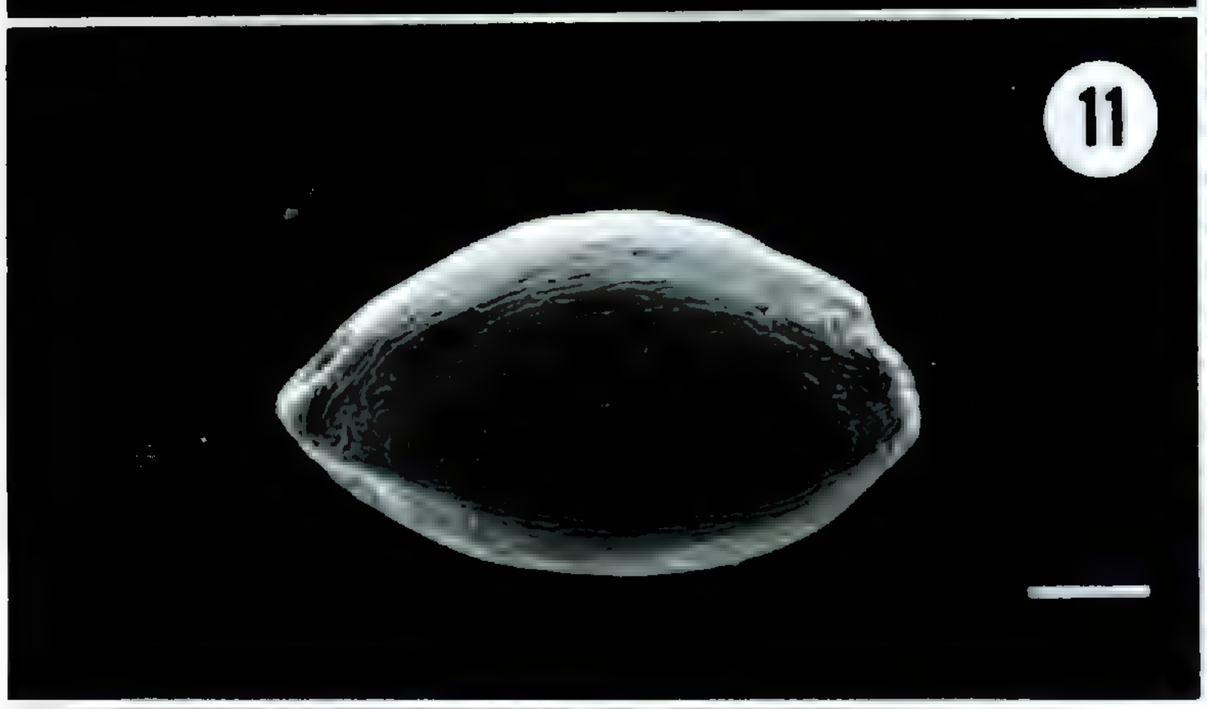


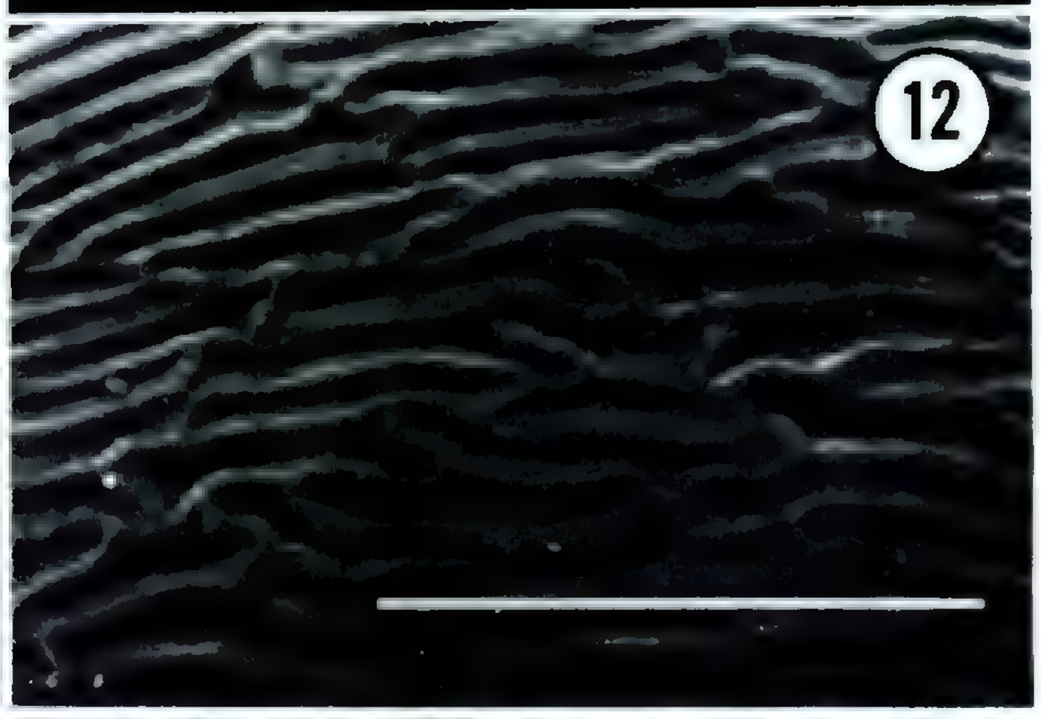


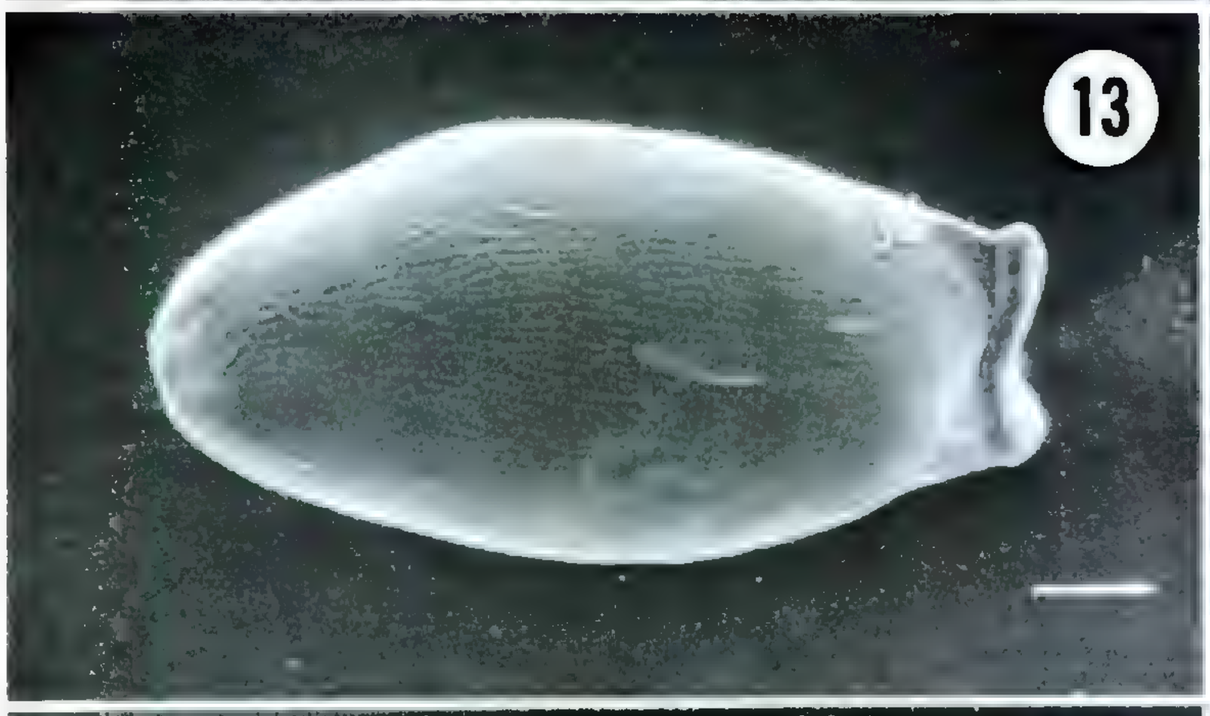


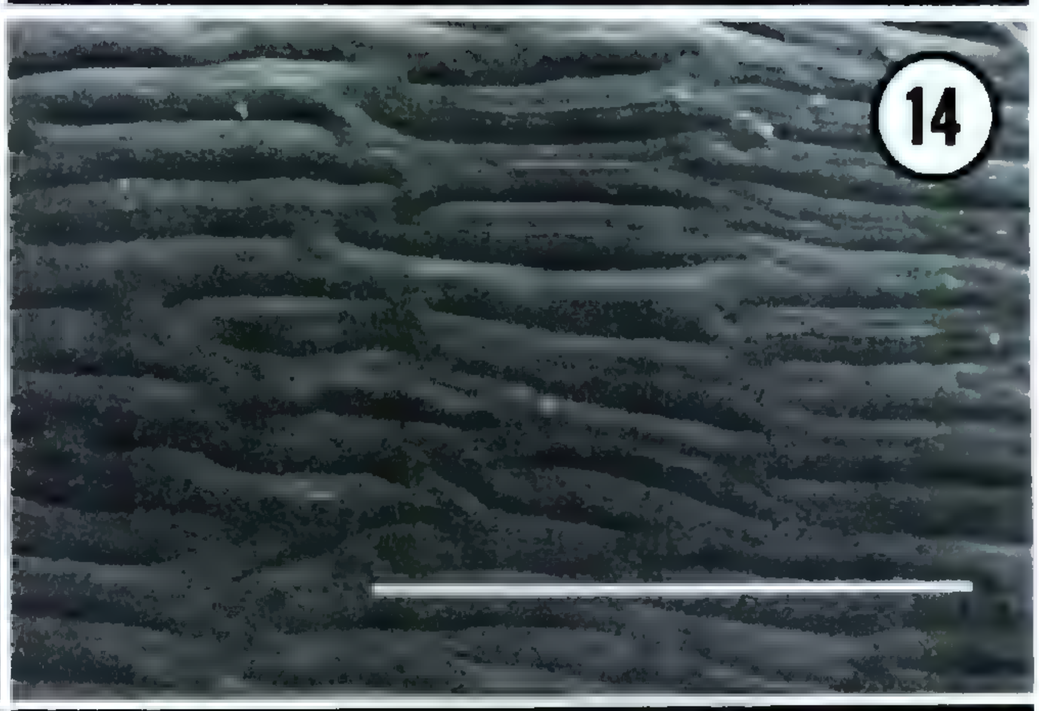
FIGURES 1–8 (bar = 100 μm). Seeds of annual *Campanula*.—Figures 1, 2. *Campanula angustiflora*.—1. Seed (S59).—2. Seed coat (S59).—Figures 3, 4. *C. griffinii*.—3. Seed (S85).—4. Seed coat (S28).—Figures 5, 6. *C. exigua*.—5. Seed (S64).—6. Seed coat (S64).—Figures 7, 8. *C. sharsmithiae*.—7. Seed (S66).—8. Seed coat (S66).

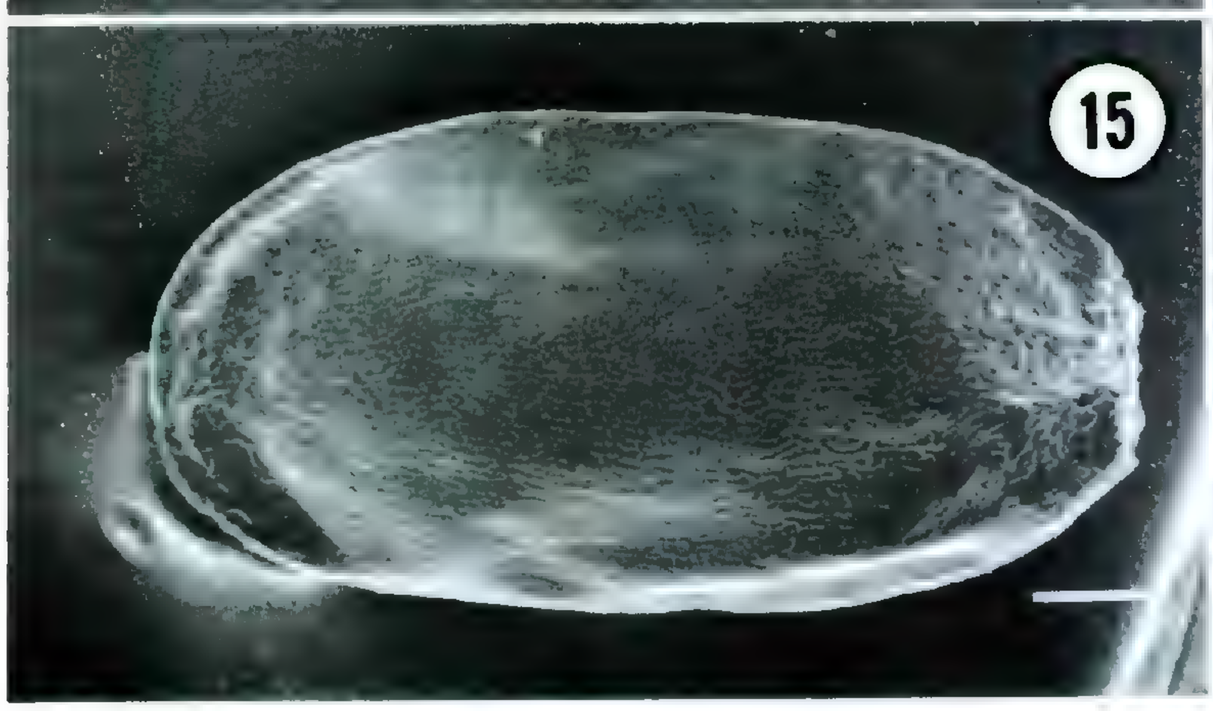




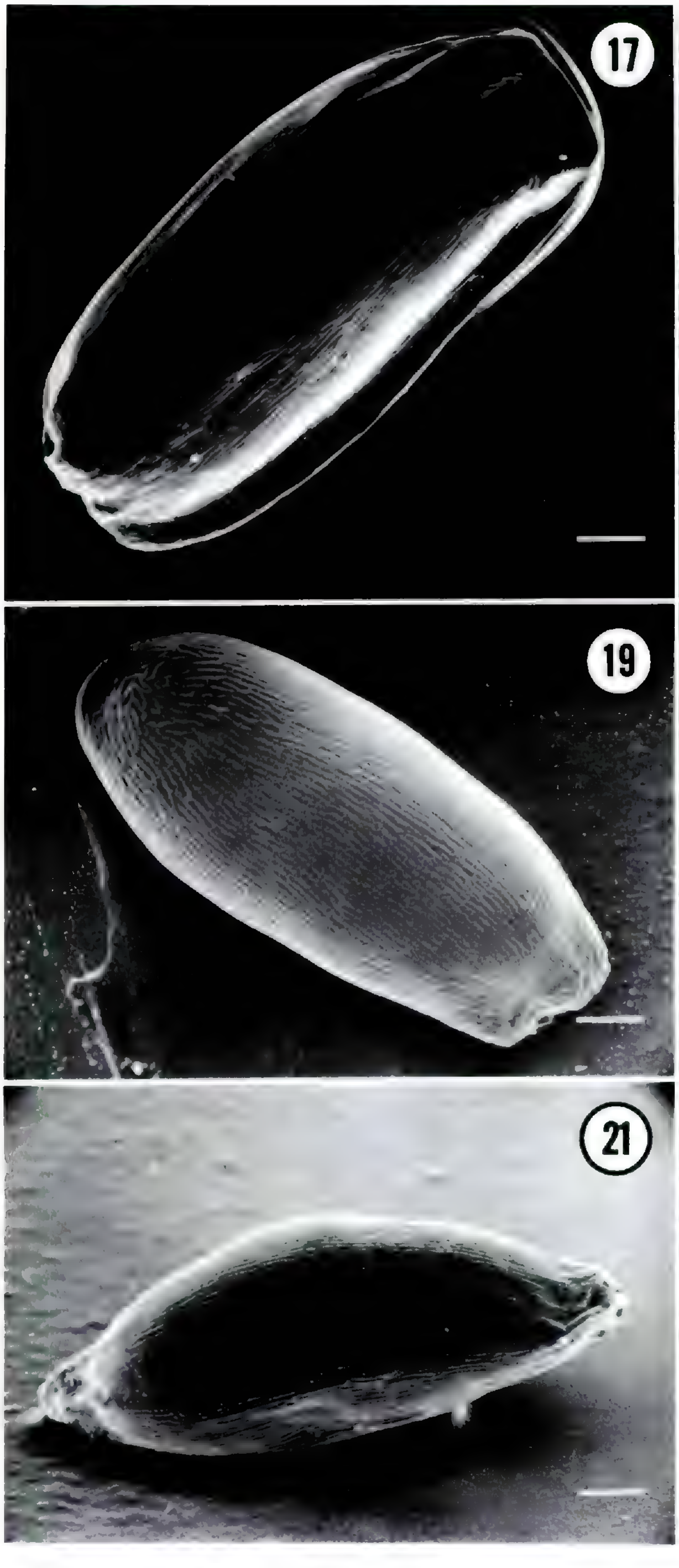


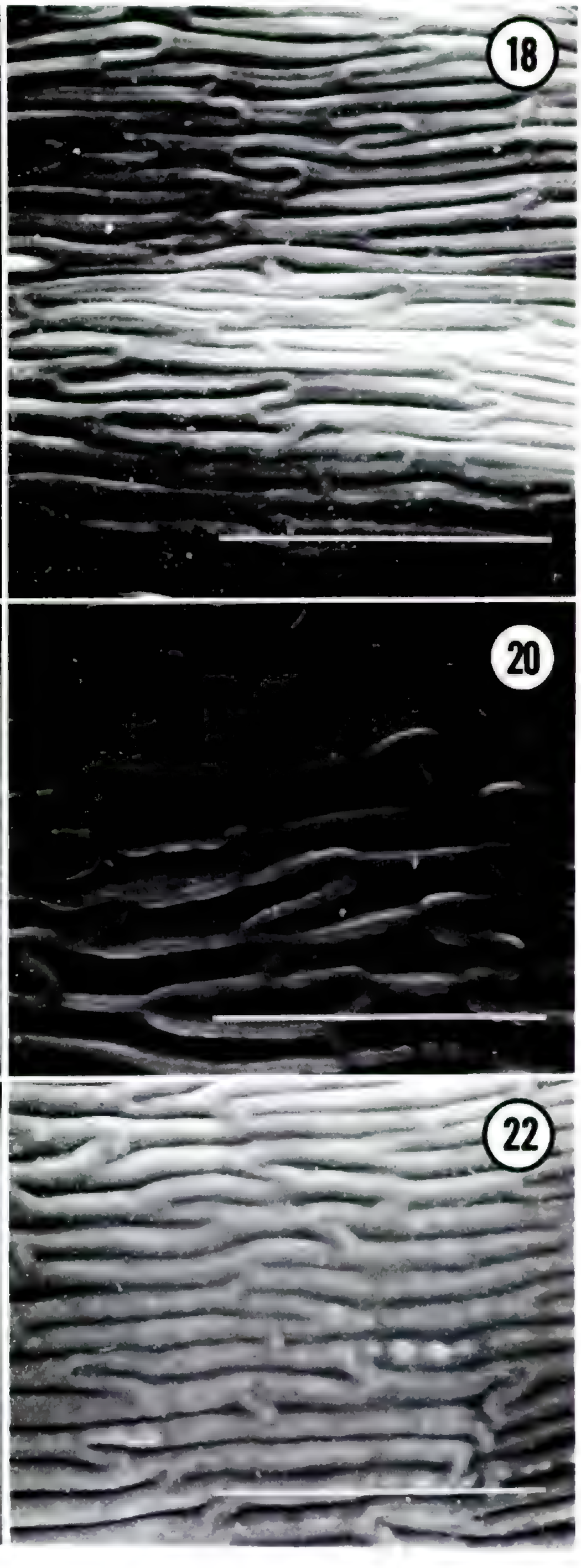






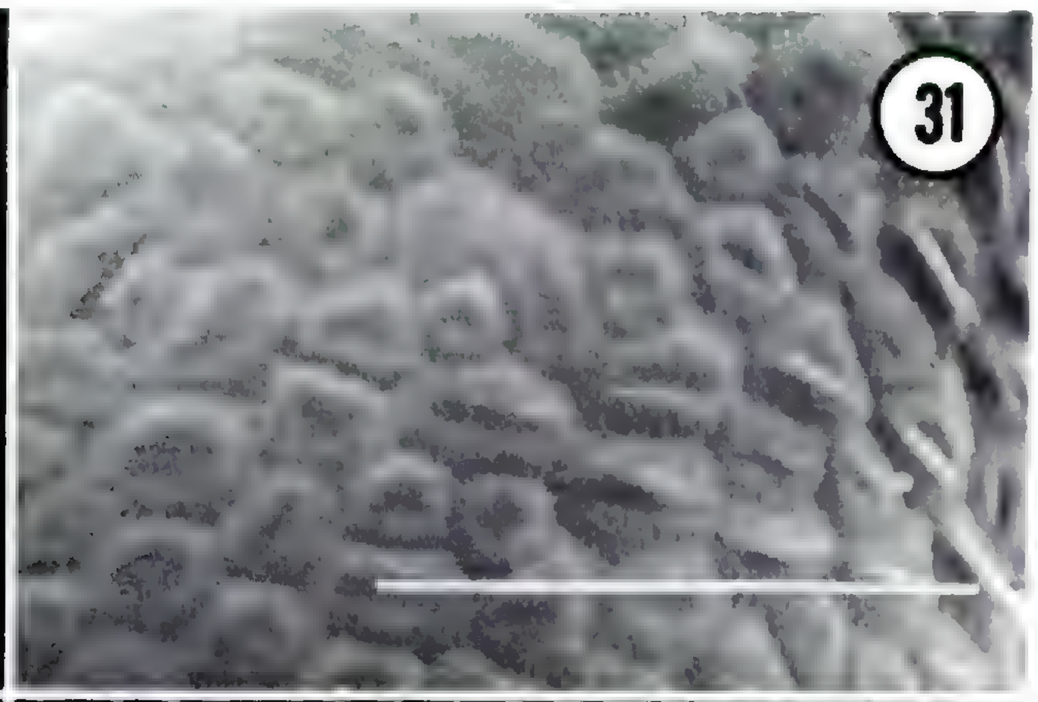
FIGURES 9–16 (bar = 100 μm). Seeds of perennial *Campanula*.—Figures 9, 10. *Campanula scabrella*.—9. Seed (S65).—10. Seed coat (S65).—Figures 11, 12. *C. parryi*.—11. Seed (S27).—12. Seed coat (S27).—Figures 13, 14. *C. piperi*.—13. Seed (S83).—14. Seed coat (S83).—Figures 15, 16. *C. aurita*.—15. Seed (S86).—16. Seed coat (S86).

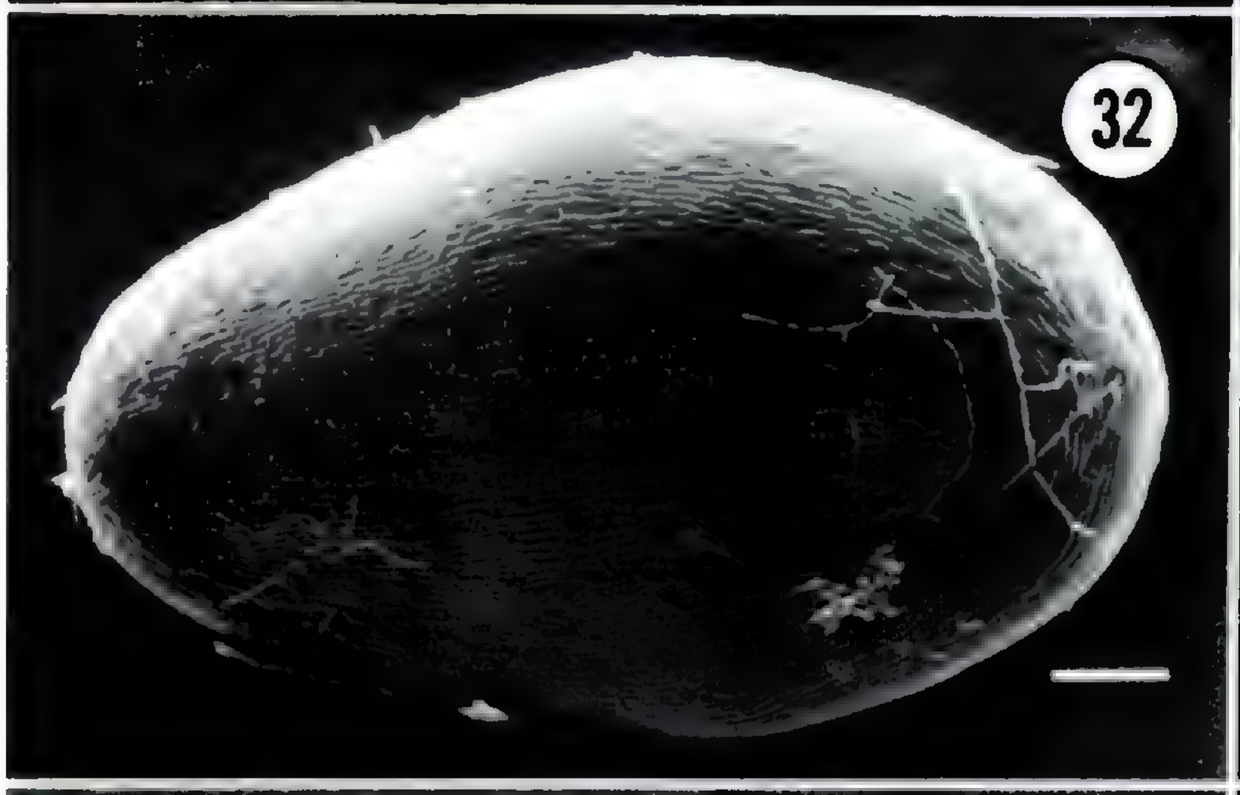




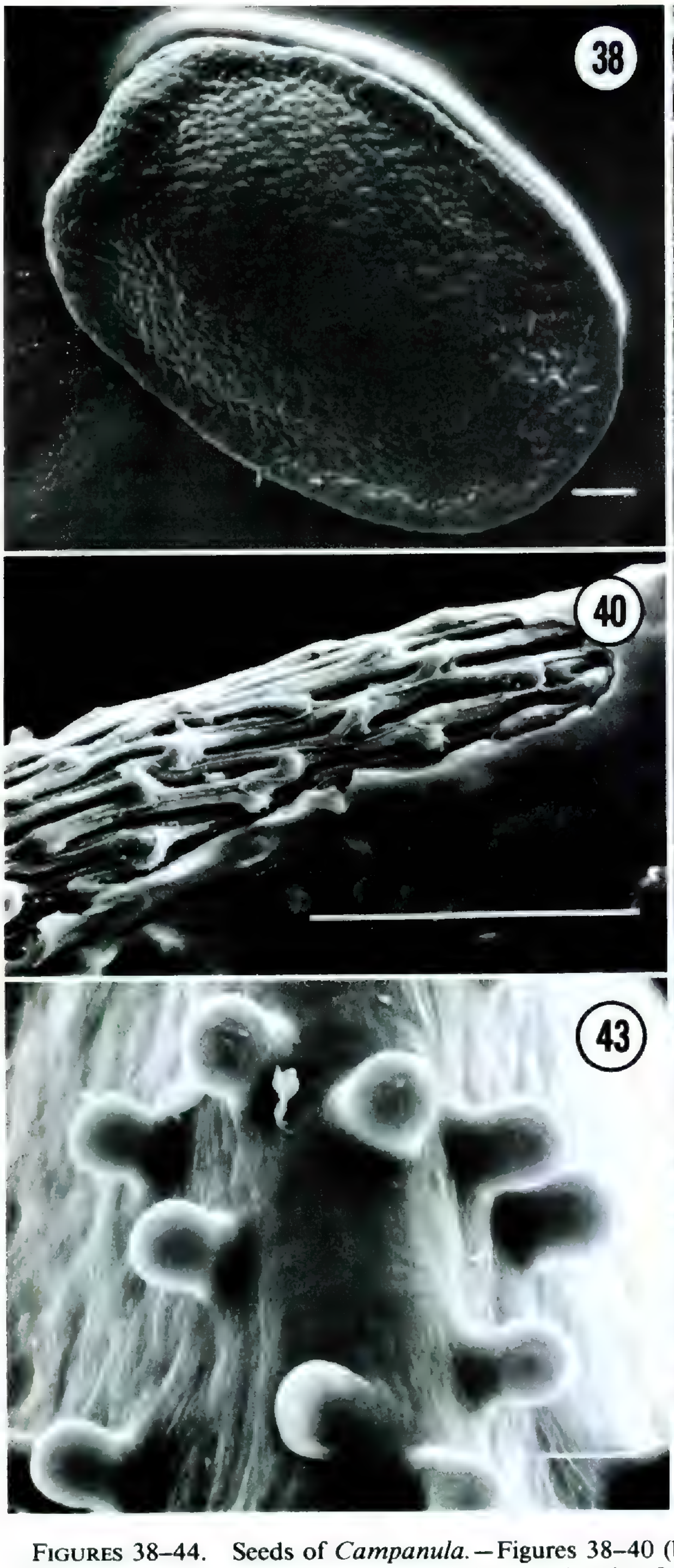
FIGURES 17–22 (bar = 100 μm). Seeds of perennial *Campanula*.—Figures 17, 18. *Campanula uniflora*.—17. Seed (S02).—18. Seed coat (S04).—Figures 19, 20. *C. rotundifolia* s.l.—19. Seed (S89).—20. Seed coat (S89).—Figures 21, 22. *C. lasiocarpa*.—21. Seed (S25).—22. Seed coat (S25).

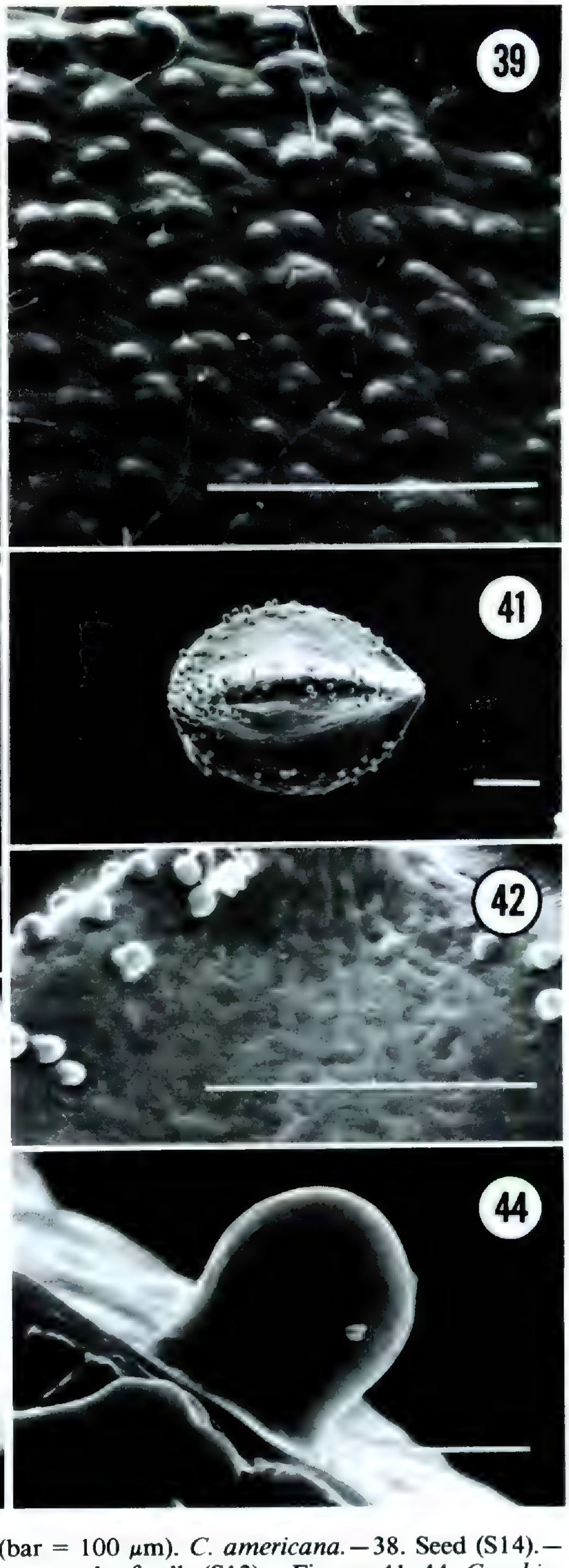
FIGURES 23–29 (bar = 100 μm). Seeds of *Campanula* and *Asyneuma*.—Figures 23, 24. *Campanula prenanthoides* (*Asyneuma prenanthoides*).—23. Seed (S08).—24. Seed coat (S08).—Figures 25–27. *C. scouleri*.—25. Seed (S05).—26. Seed coat with tangential walls collapsed (S05).—27. Seed coat with tangential walls uncollapsed (S05).—Figures 28, 29. *Asyneuma canescens*.—28. Seed (S72).—29. Seed coat (S72).



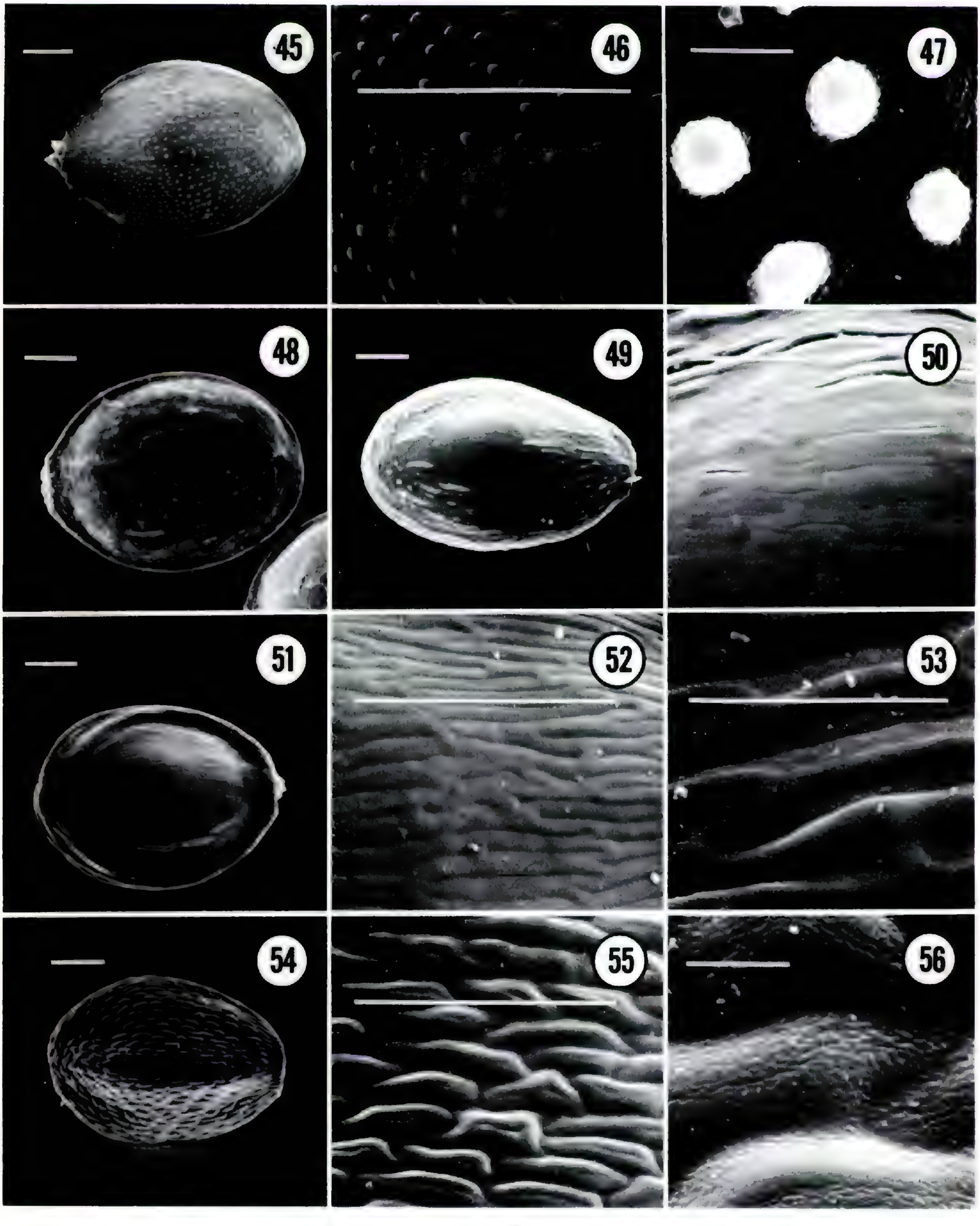


FIGURES 30–37 (bar = 100 μm). Seeds of *Campanula*.—Figures 30, 31. *Campanula aparinoides*.—30. Seed (S62).—31. Seed coat (S60).—Figures 32, 33. *C. californica*.—32. Seed (S17).—33. Seed coat (S17).—Figures 34, 35. *C. divaricata*.—34. Seed (S19).—35. Seed coat (S18).—Figures 36, 37. *C. floridana*.—36. Seed (S21).—37. Seed coat (S21).

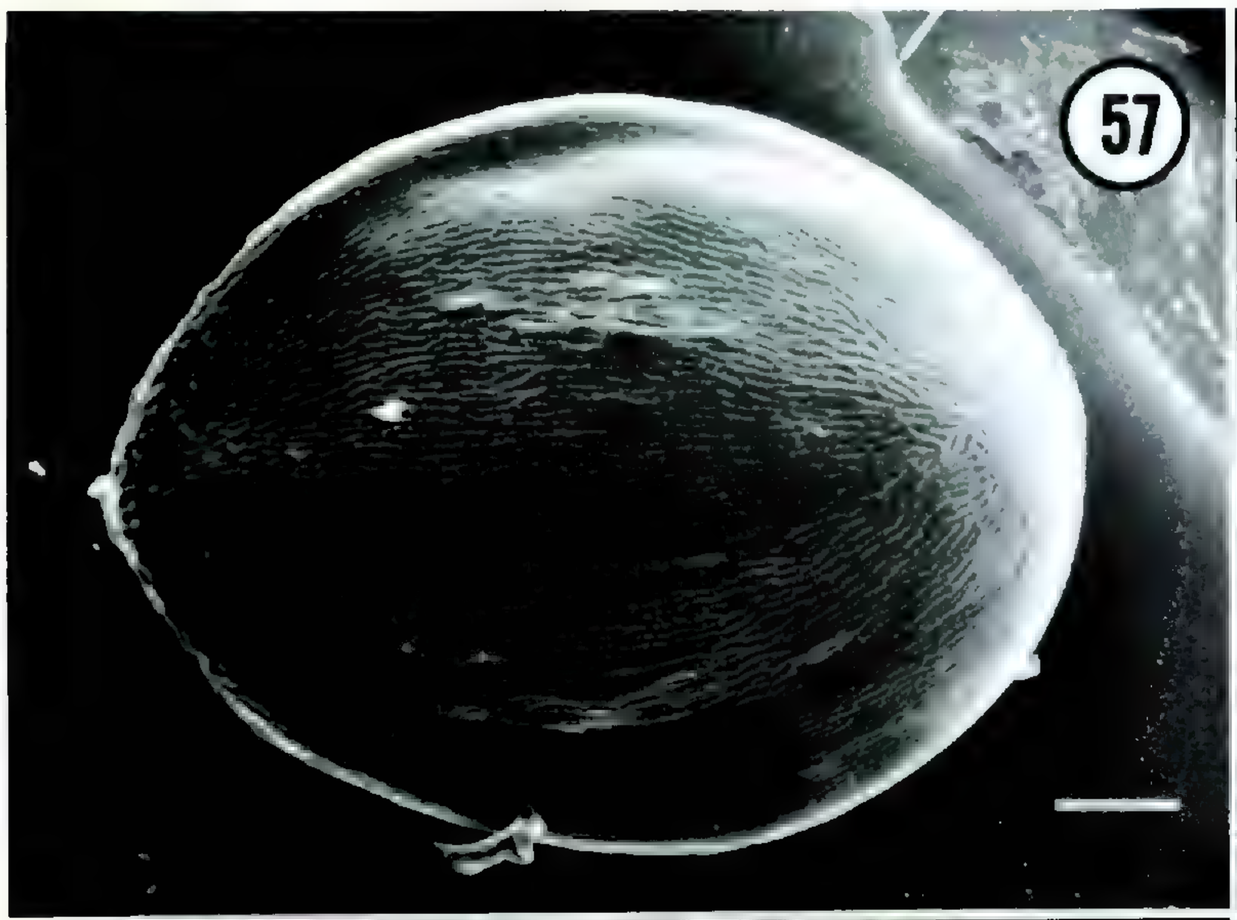


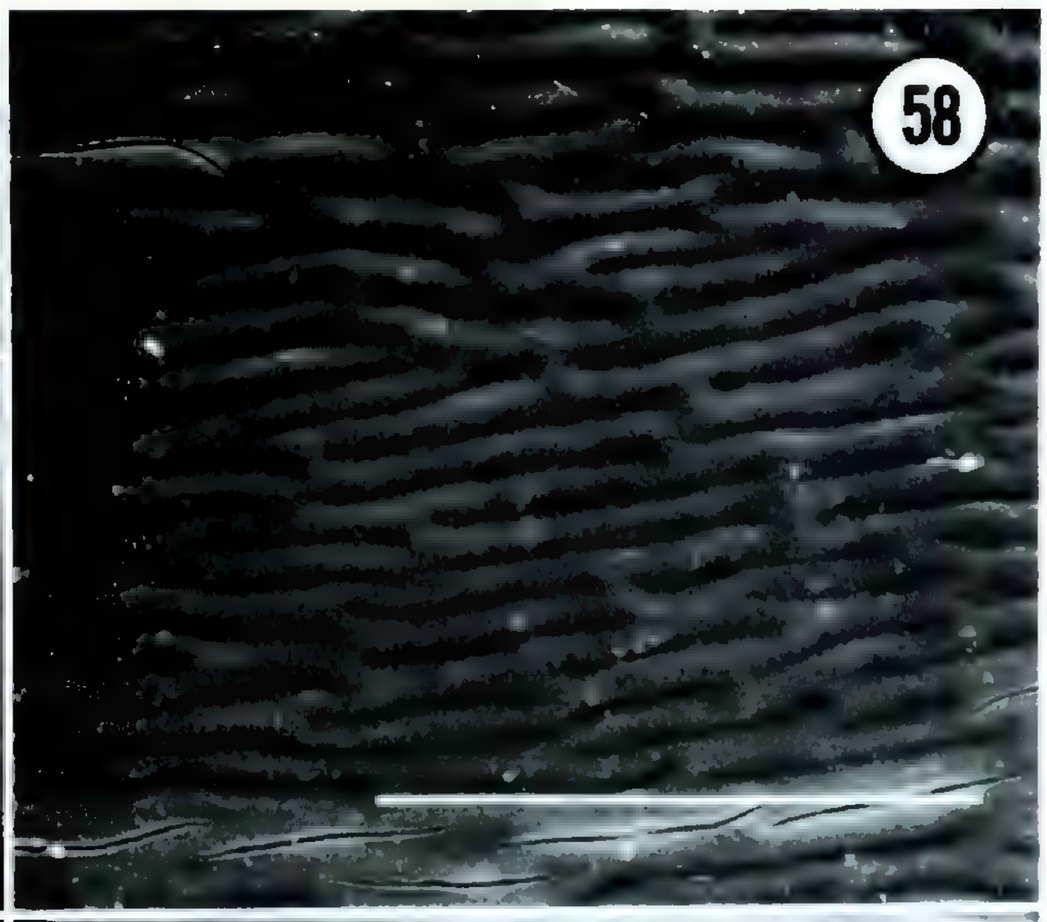


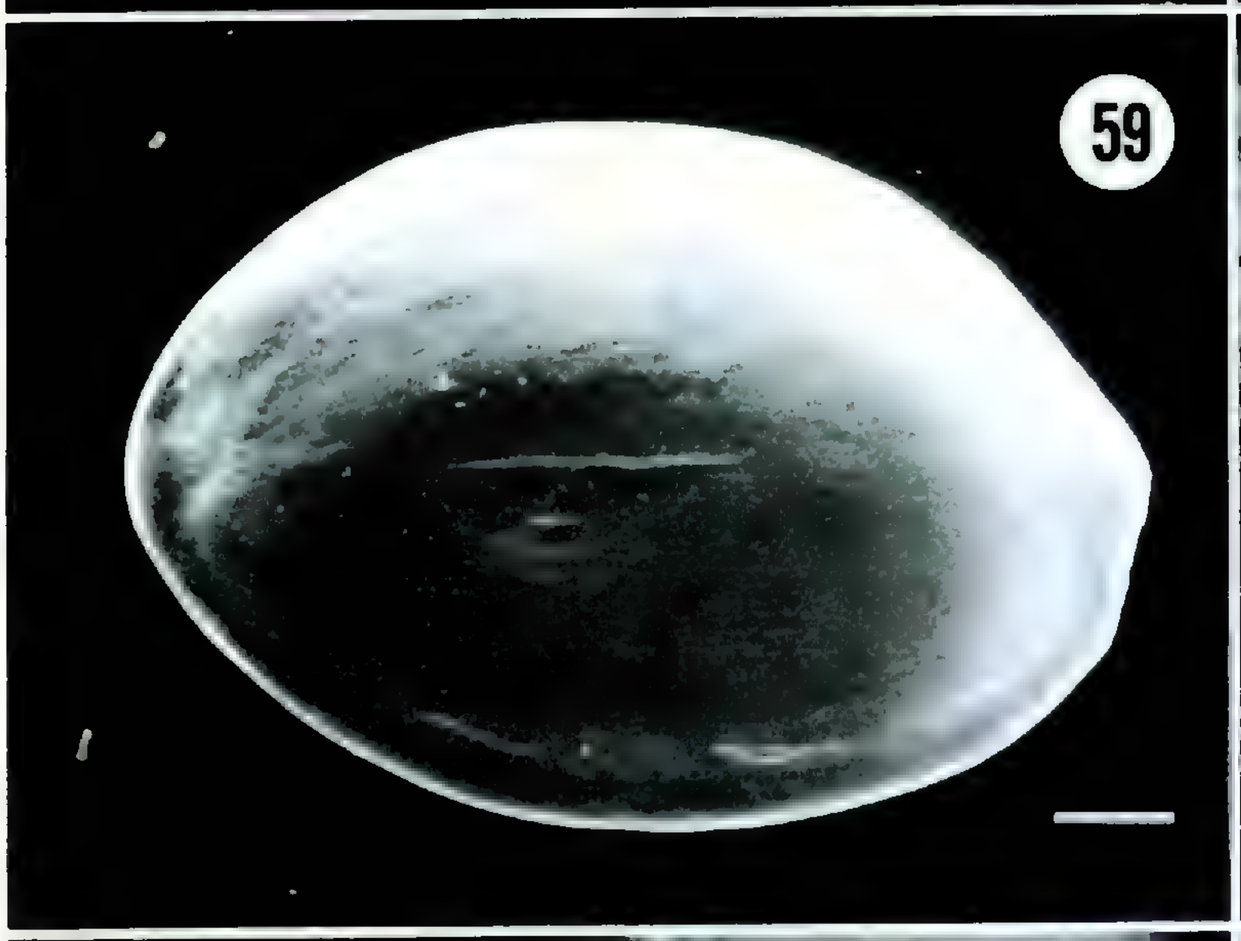
FIGURES 38–44. Seeds of *Campanula*.—Figures 38–40 (bar = 100 μm). *C. americana*.—38. Seed (S14).—39. Seed coat (S14).—40. Seed coat peeled away showing framework of cells (S13).—Figures 41–44. *C. robinsiae*.—41. Seed (S90) (bar = 100 μm).—42. Seed coat (S090) (bar = 100 μm).—43. Seed coat (S090) (bar = 10 μm).—44. Seed coat showing 1 papilla (S090) (bar = 10 μm).

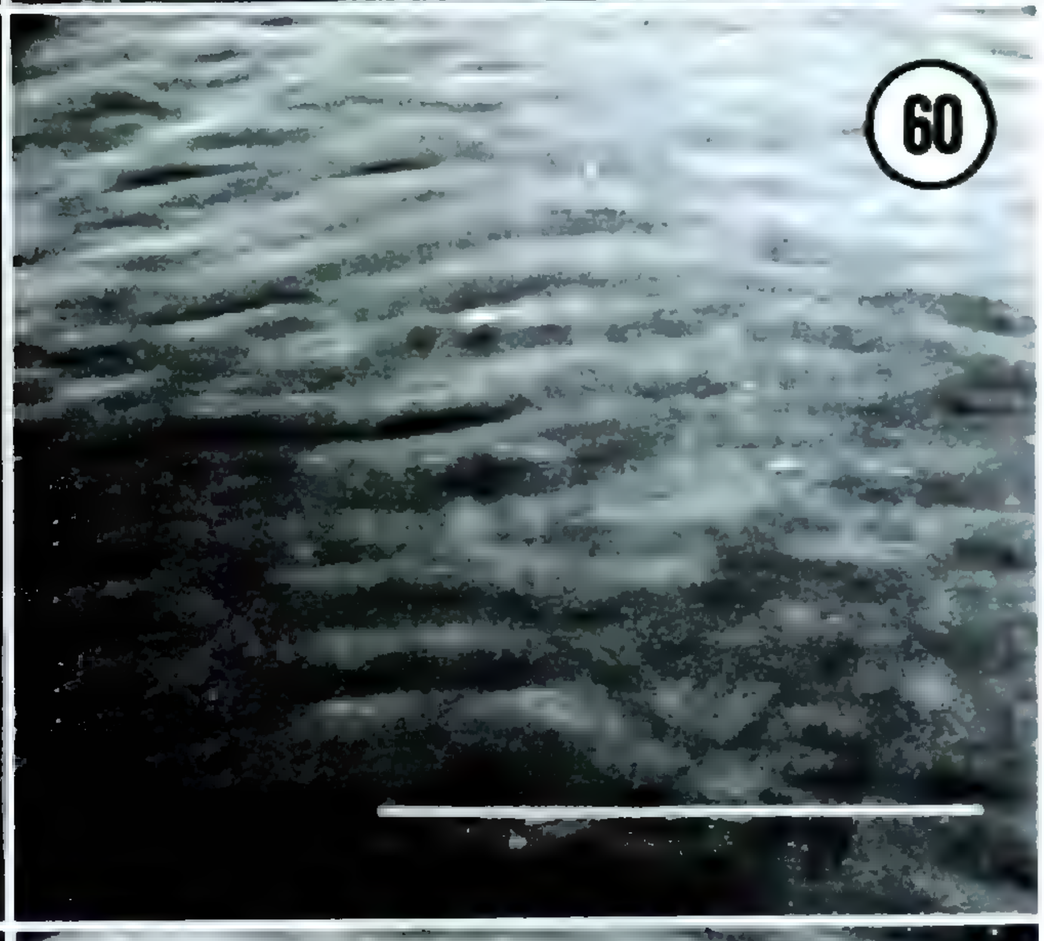


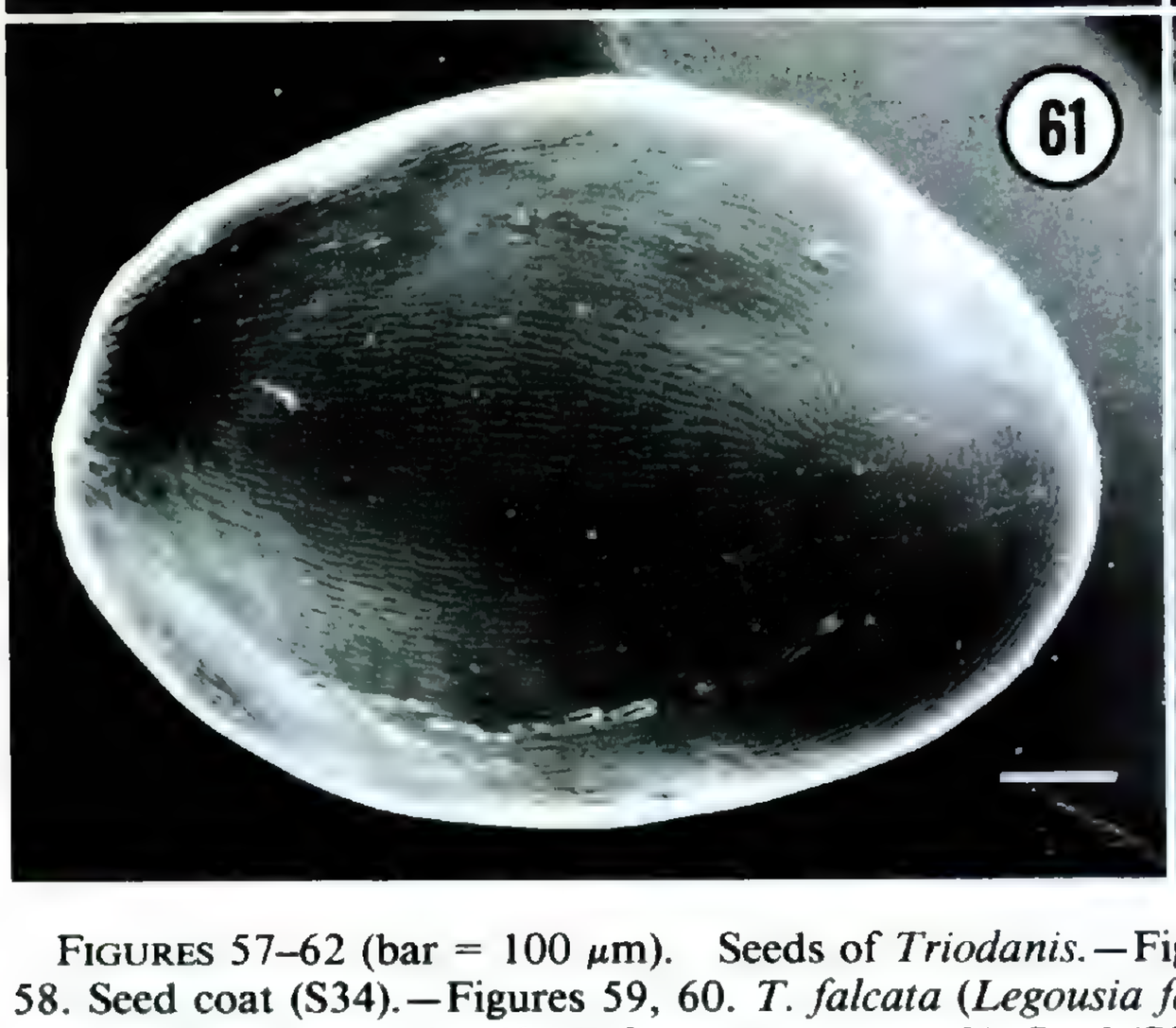
FIGURES 45–56. Seeds of *Triodanis*.—Figures 45–48. *Triodanis perfoliata*.—45. Seed of papillate type (S44) (bar = 100 μm).—46. Seed coat of papillate type (S44) (bar = 100 μm).—47. Seed coat of papillate type (S44) (bar = 10 μm).—48. Seed of smooth type (S43) (bar = 100 μm).—Figures 49, 50 (bar = 100 μm). *T. holzingeri*.—49. Seed (S36).—50. Seed coat (S36).—Figures 51–53. *T. biflora*.—51. Seed (S46) (bar = 100 μm).—52. Seed coat (S46) (bar = 100 μm).—53. Seed coat (S47) (bar = 10 μm).—Figures 54–56. *T. texana*.—54. Seed (S51) (bar = 100 μm).—55. Seed coat (S51) (bar = 100 μm).—56. Seed coat (S48) (bar = 10 μm).

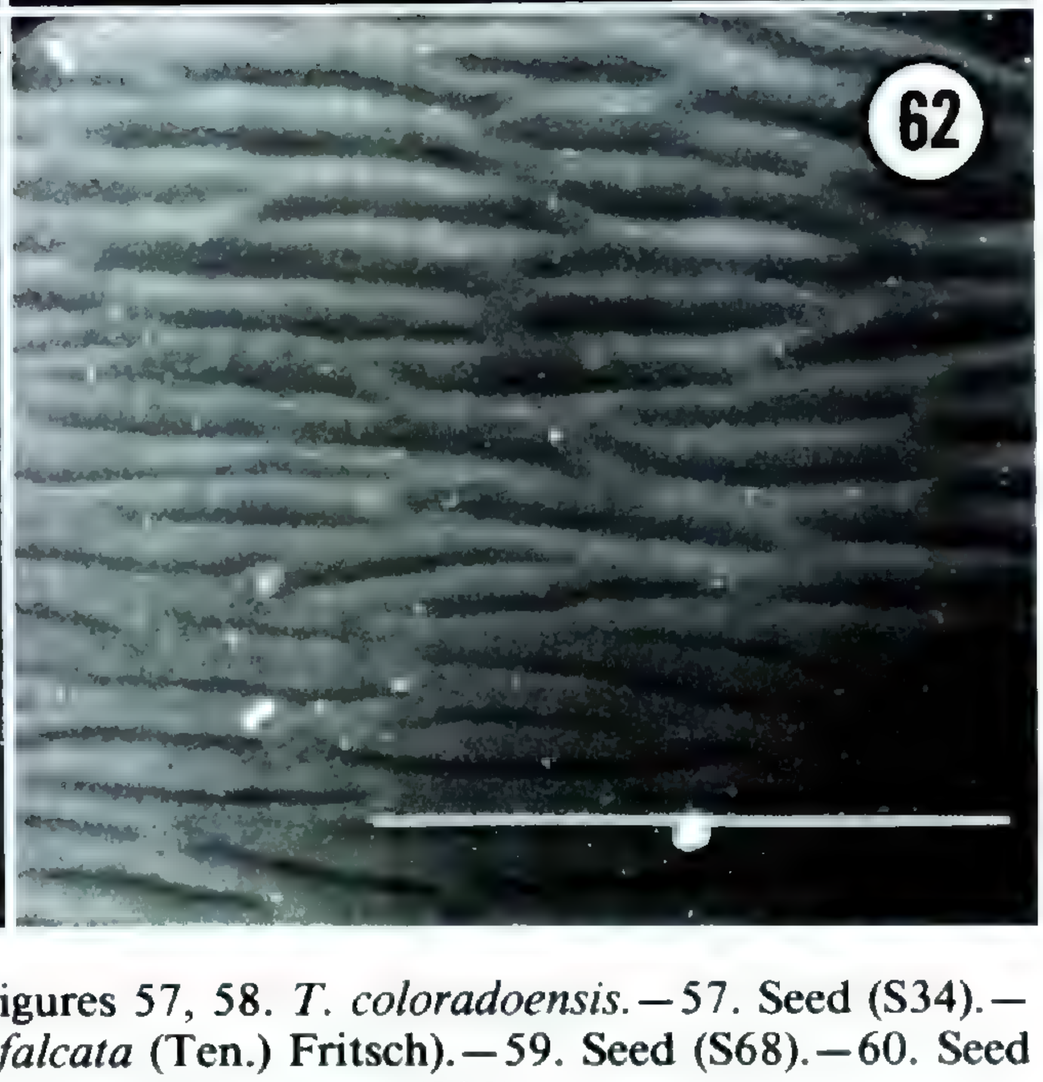




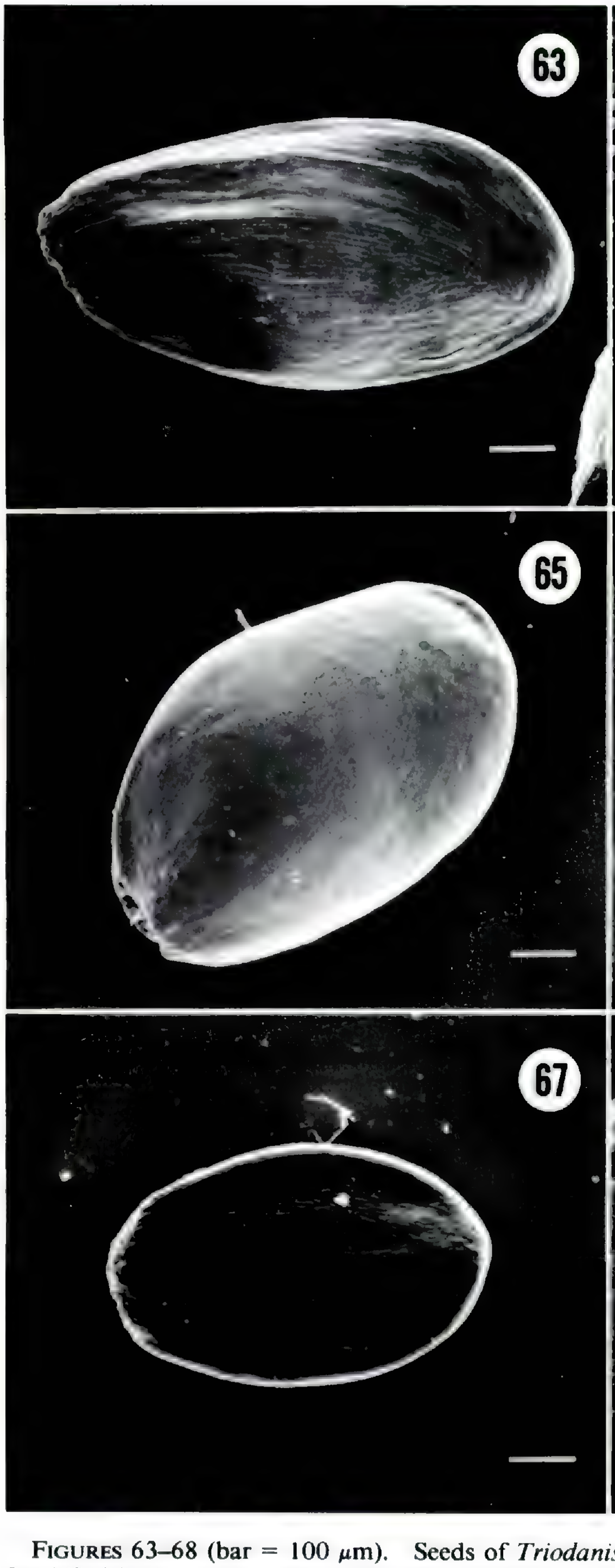


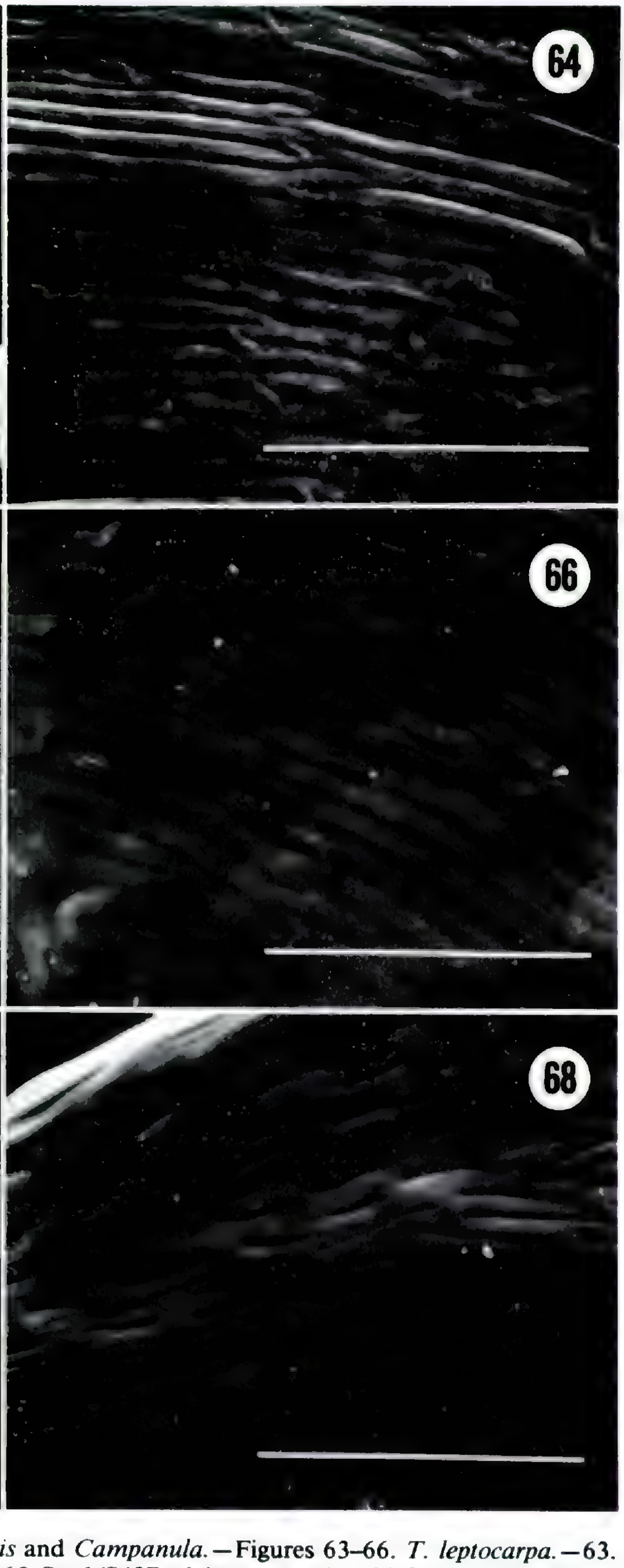




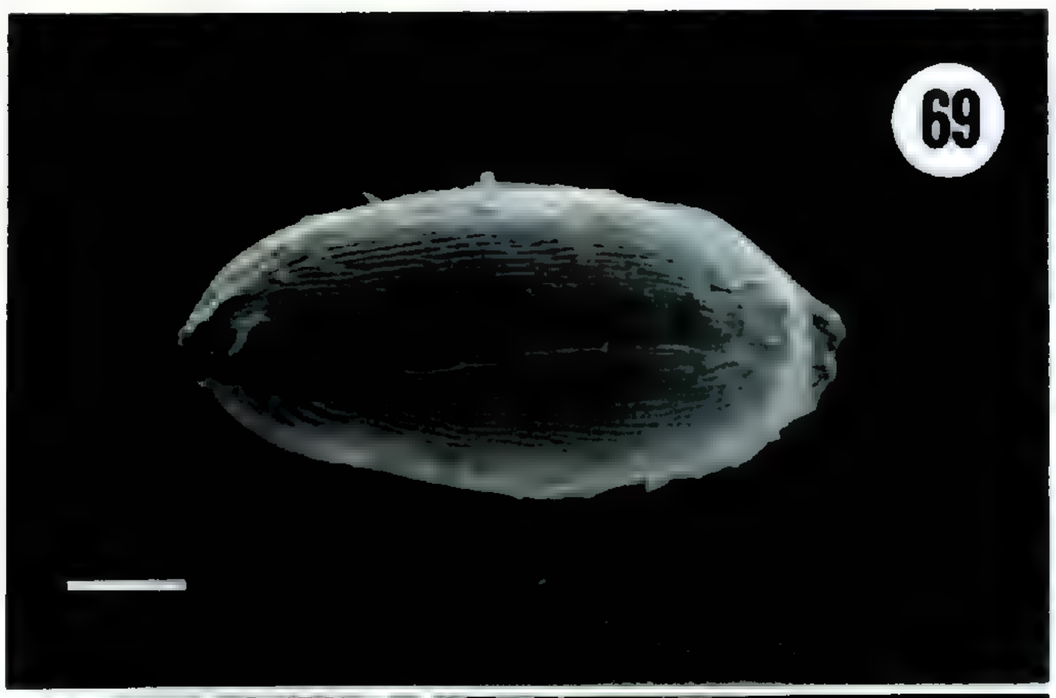


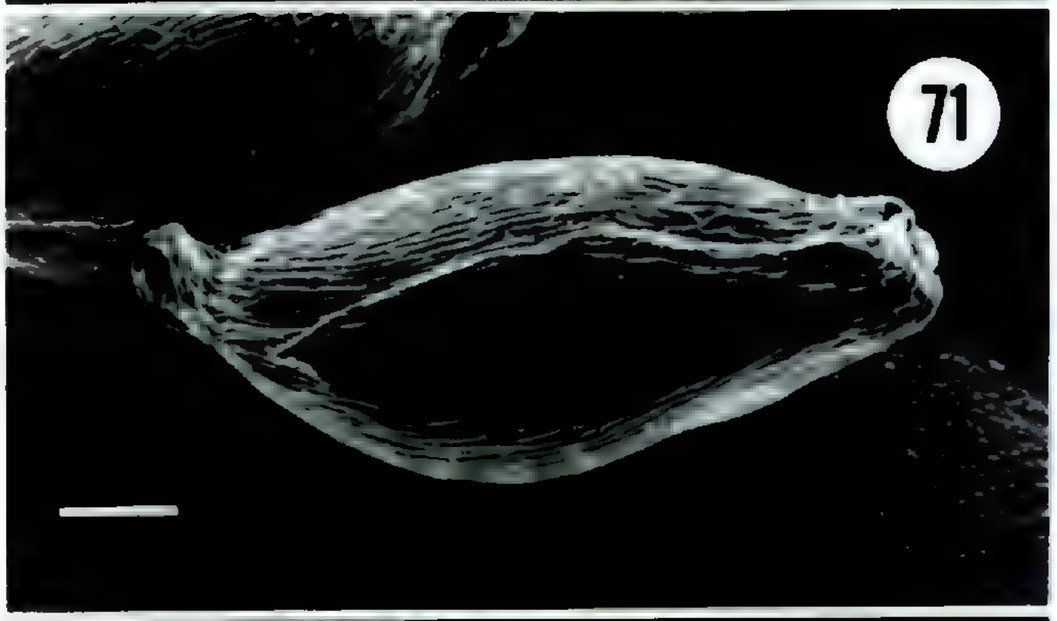
FIGURES 57–62 (bar = 100 μm). Seeds of *Triodanis*.—Figures 57, 58. *T. coloradoensis*.—57. Seed (S34).—58. Seed coat (S34).—Figures 59, 60. *T. falcata* (*Legousia falcata* (Ten.) Fritsch).—59. Seed (S68).—60. Seed coat (S68).—Figures 61, 62. *T. lamprosperma*.—61. Seed (S39).—62. Seed coat (S39).

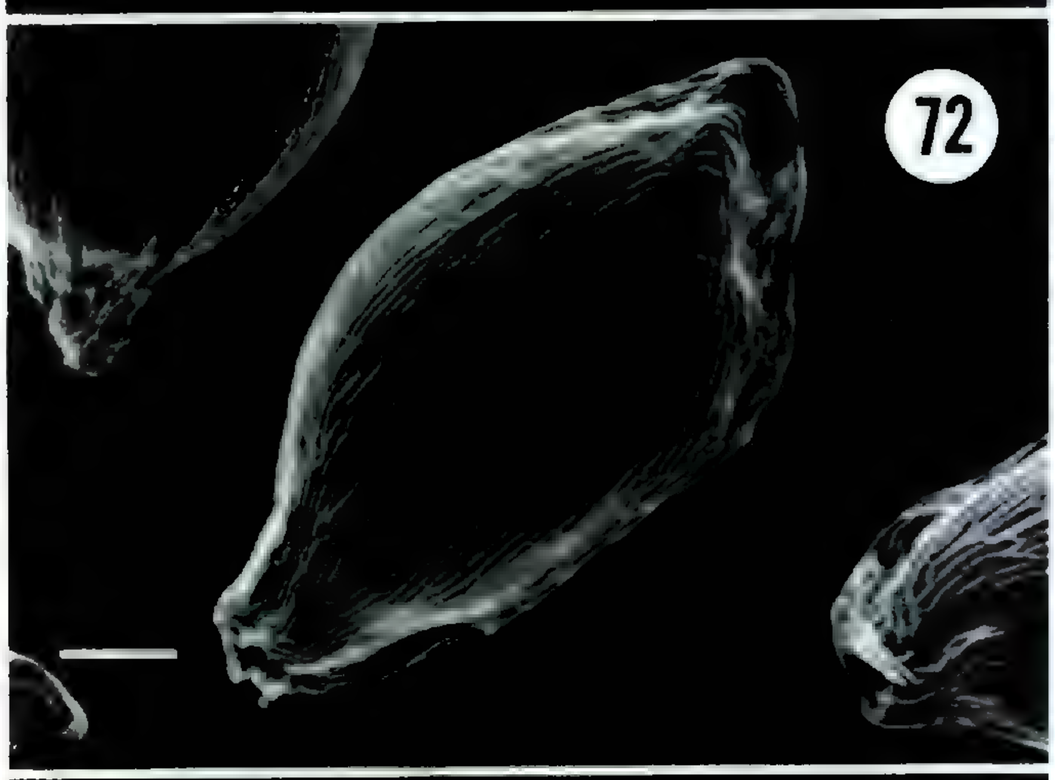


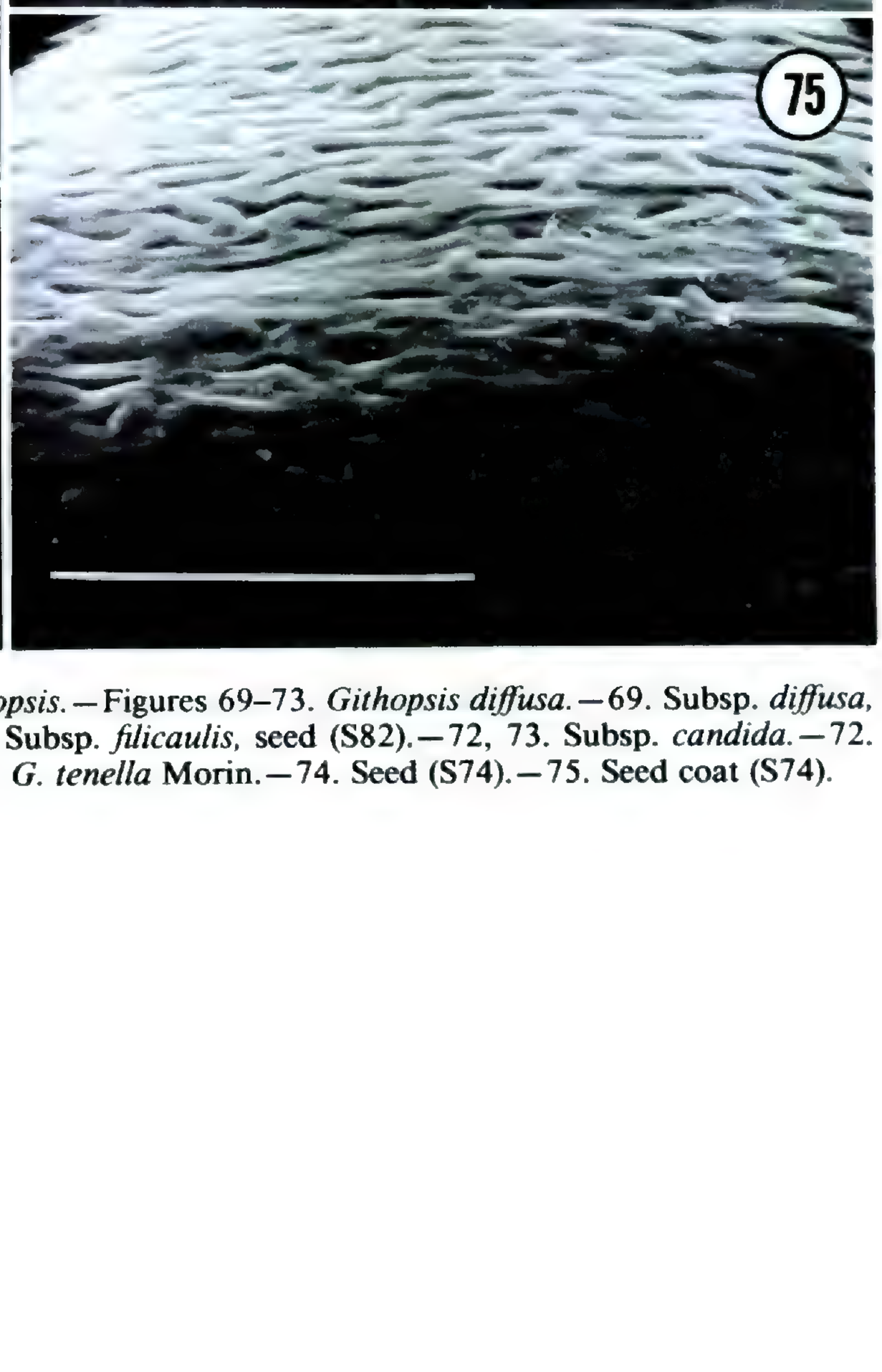


FIGURES 63–68 (bar = 100 μm). Seeds of *Triodanis* and *Campanula*.—Figures 63–66. *T. leptocarpa*.—63. Seed (S42A, chasmogamous).—64. Seed coat (S42A).—65. Seed (S42B, cleistogamous).—66. Seed coat (S42B).—Figures 67, 68. *Campanula reverchoni*.—67. Seed (S12).—68. Seed coat (S12).

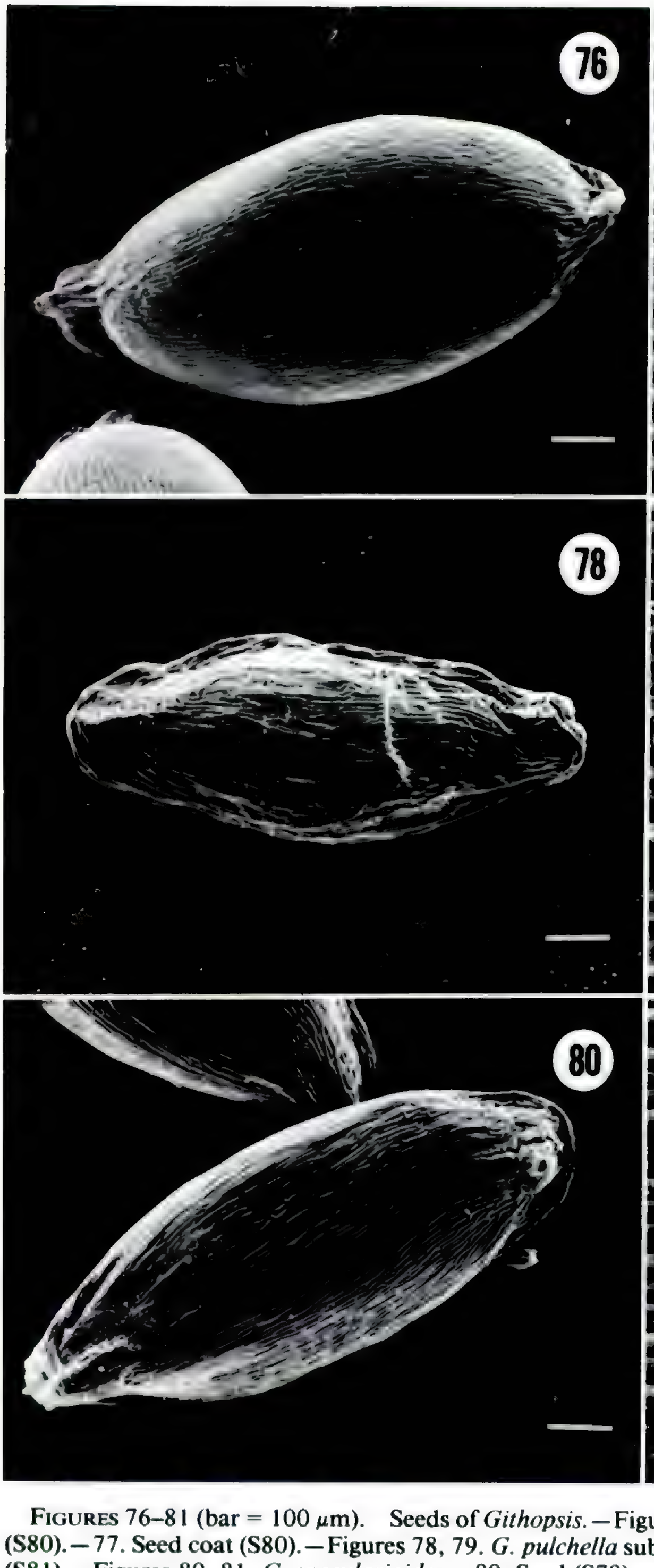




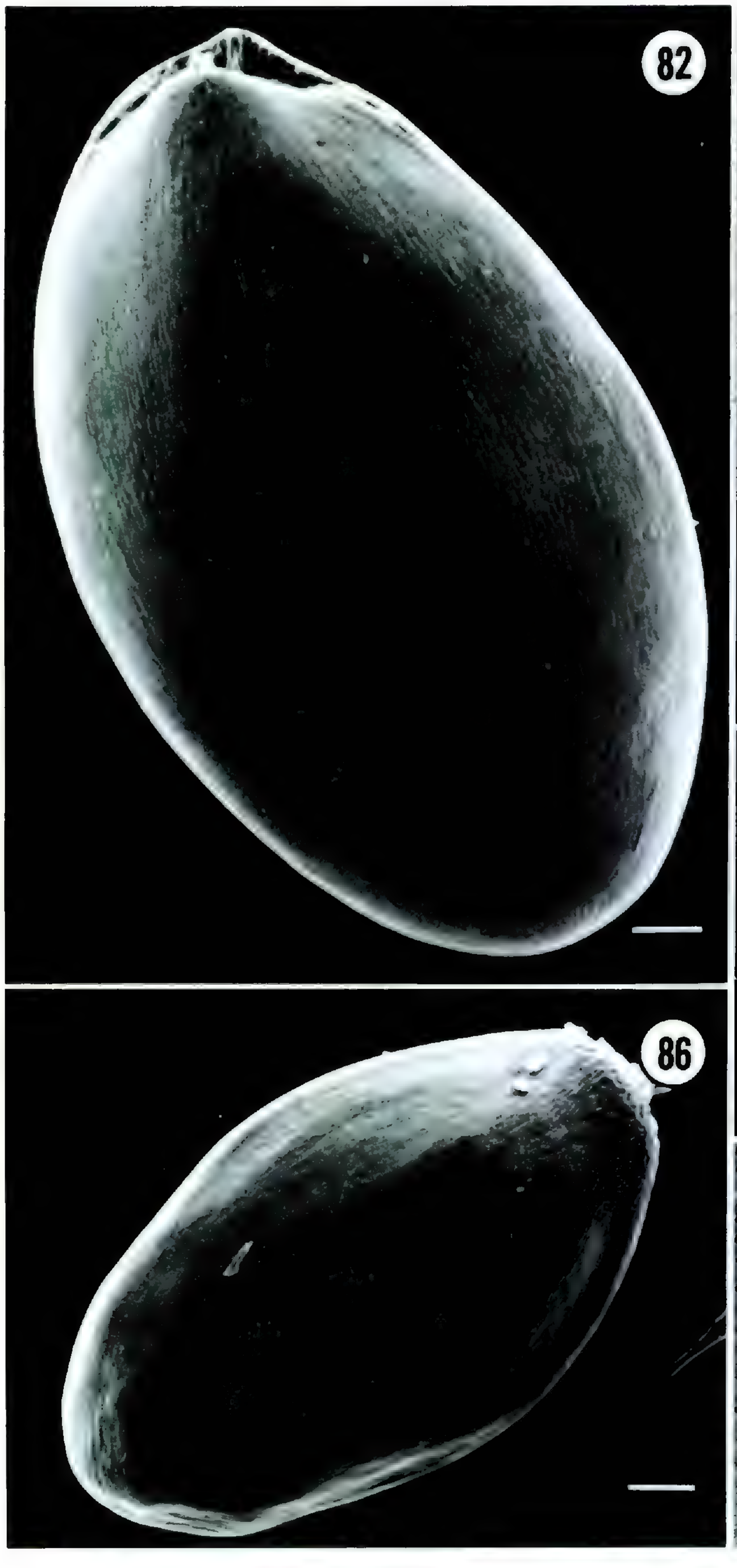


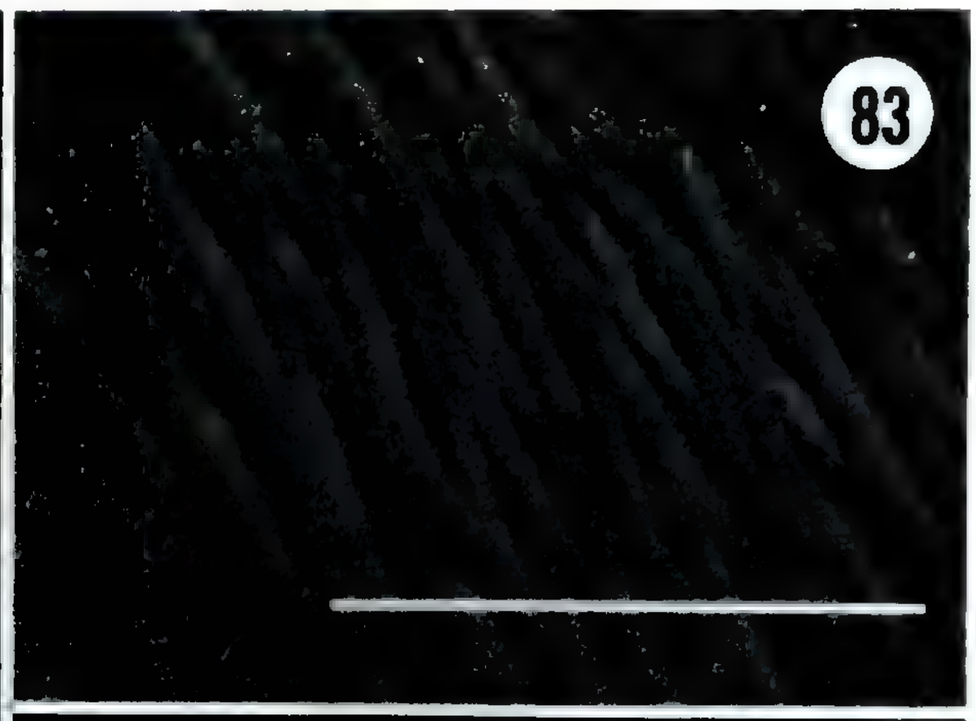


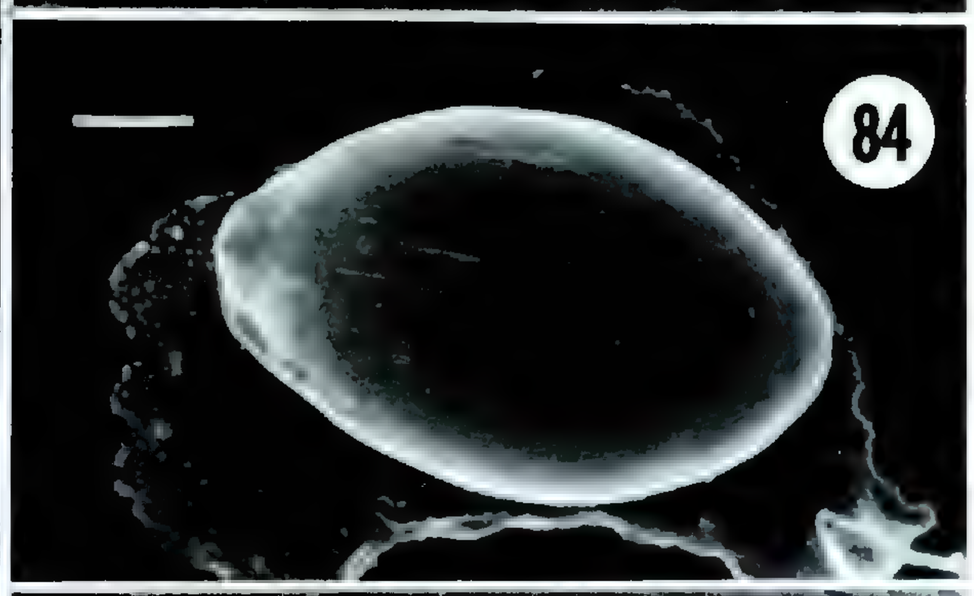
FIGURES 69–75 (bar = 100 μm). Seeds of *Githopsis*.—Figures 69–73. *Githopsis diffusa*.—69. Subsp. *diffusa*, seed (S78).—70. Subsp. *robusta*, seed (S77).—71. Subsp. *filicaulis*, seed (S82).—72, 73. Subsp. *candida*.—72. Seed (S79).—73. Seed coat (S79).—Figures 74, 75. *G. tenella* Morin.—74. Seed (S74).—75. Seed coat (S74).

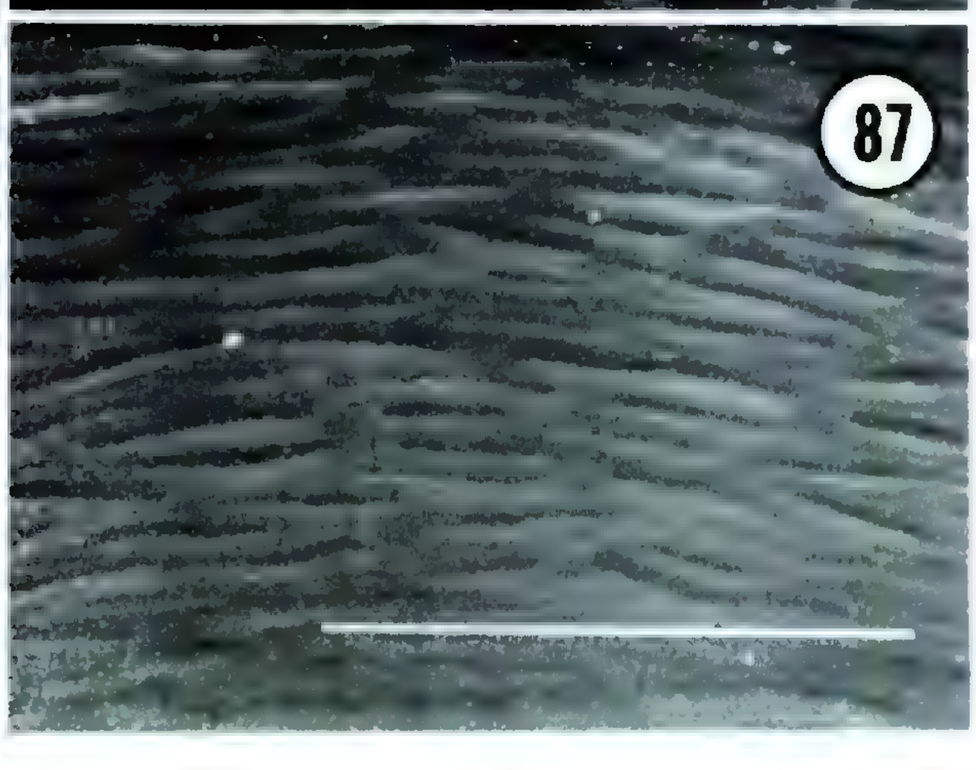


FIGURES 76–81 (bar = 100 μm). Seeds of *Githopsis*.—Figures 76, 77. *G. pulchella* subsp. *pulchella*.—76. Seed (S80).—77. Seed coat (S80).—Figures 78, 79. *G. pulchella* subsp. *serpentinicola*.—78. Seed (S81).—79. Seed coat (S81).—Figures 80, 81. *G. specularioides*.—80. Seed (S79).—81. Seed coat (S79).

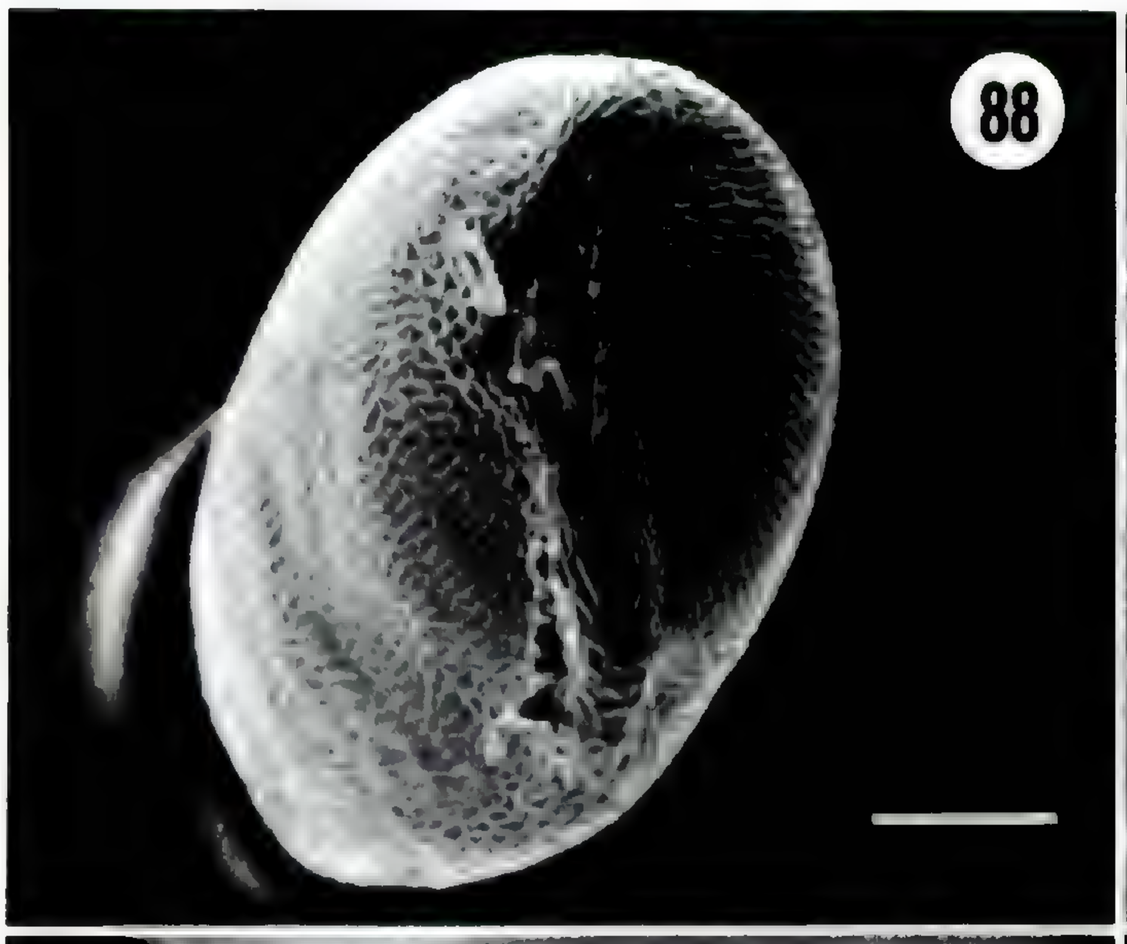


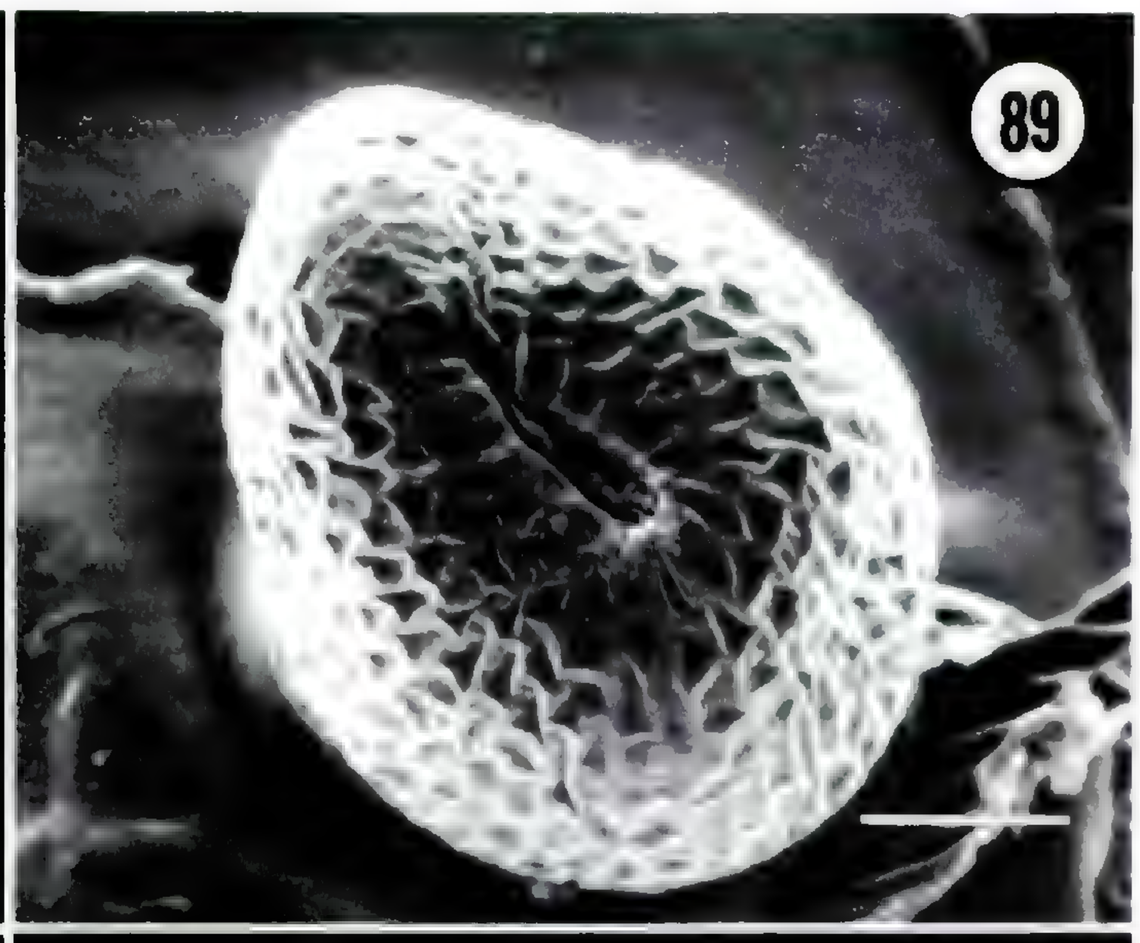


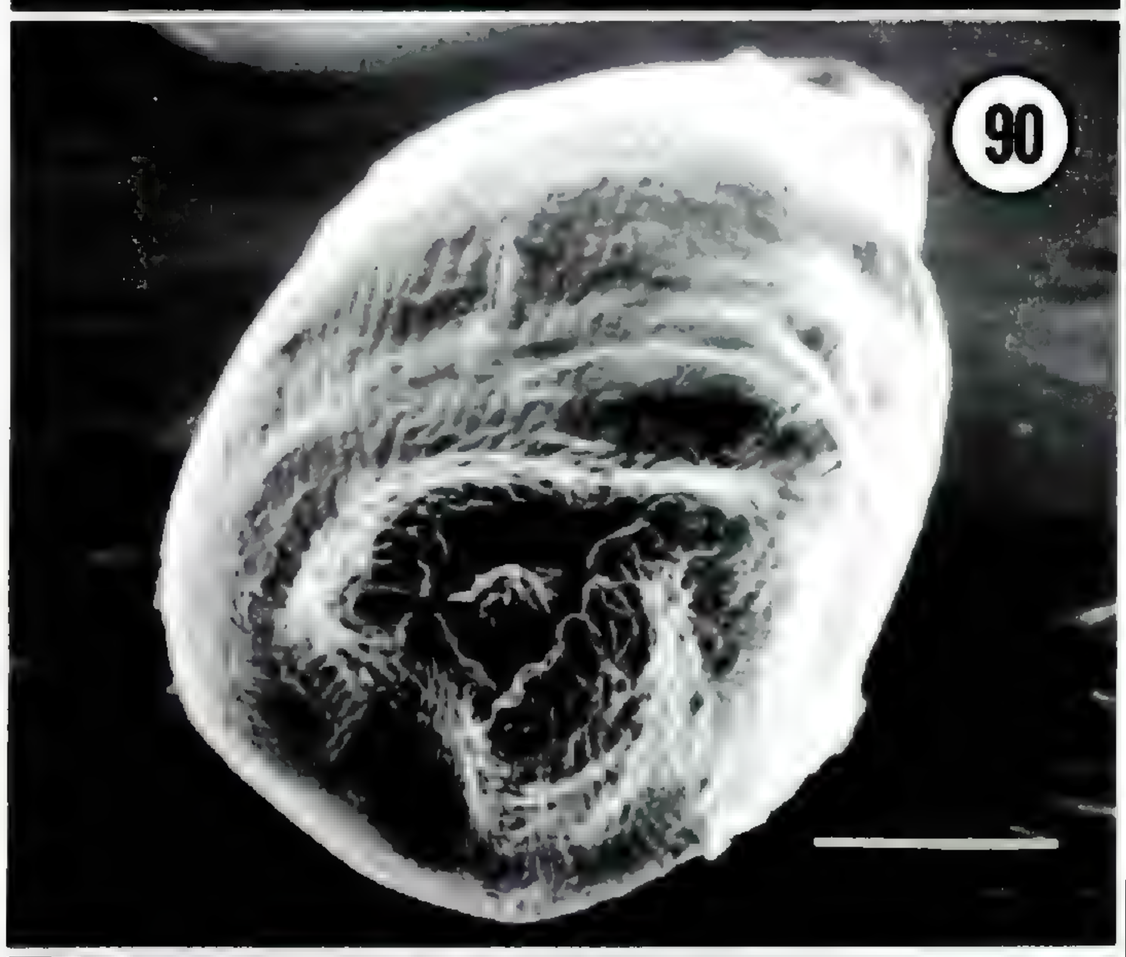


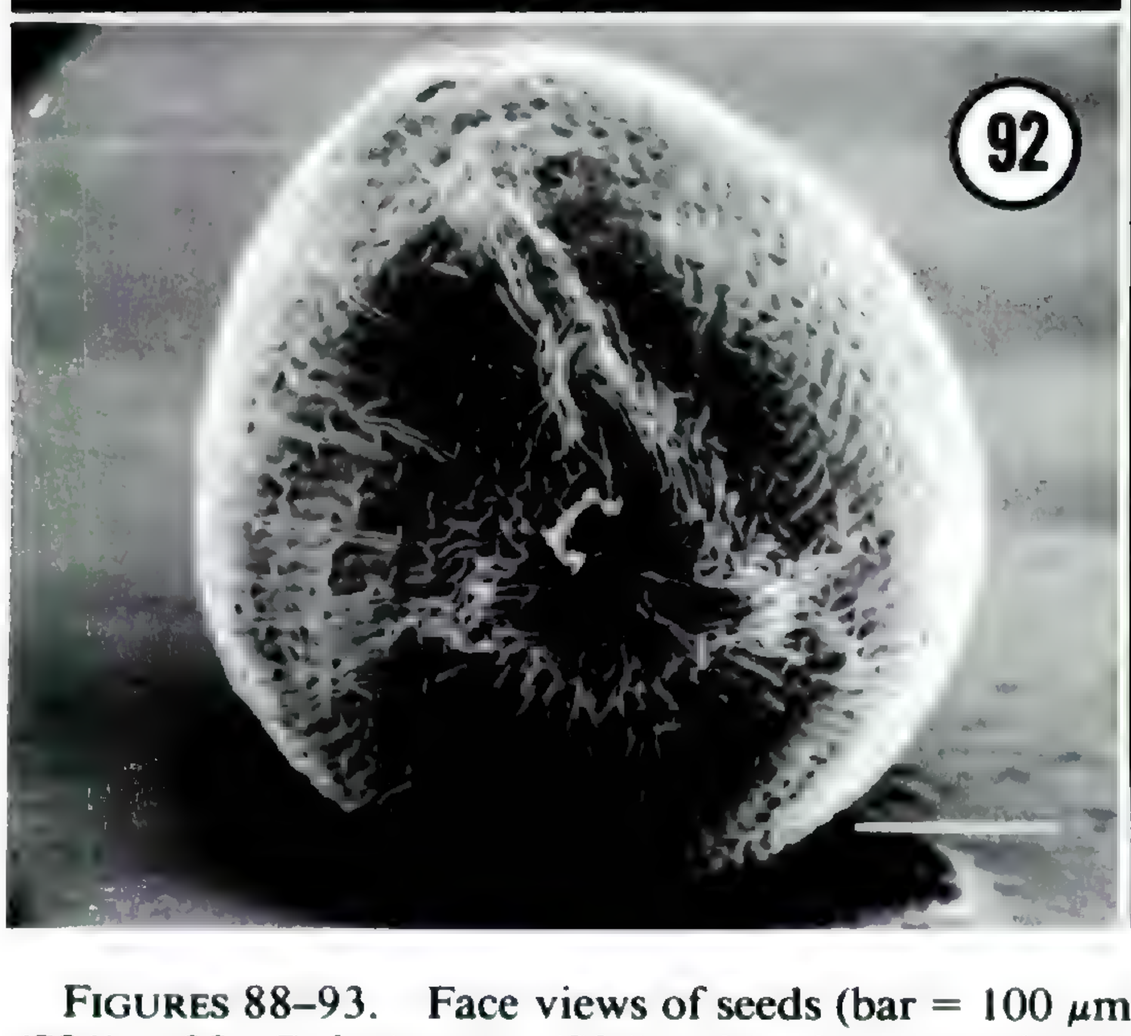


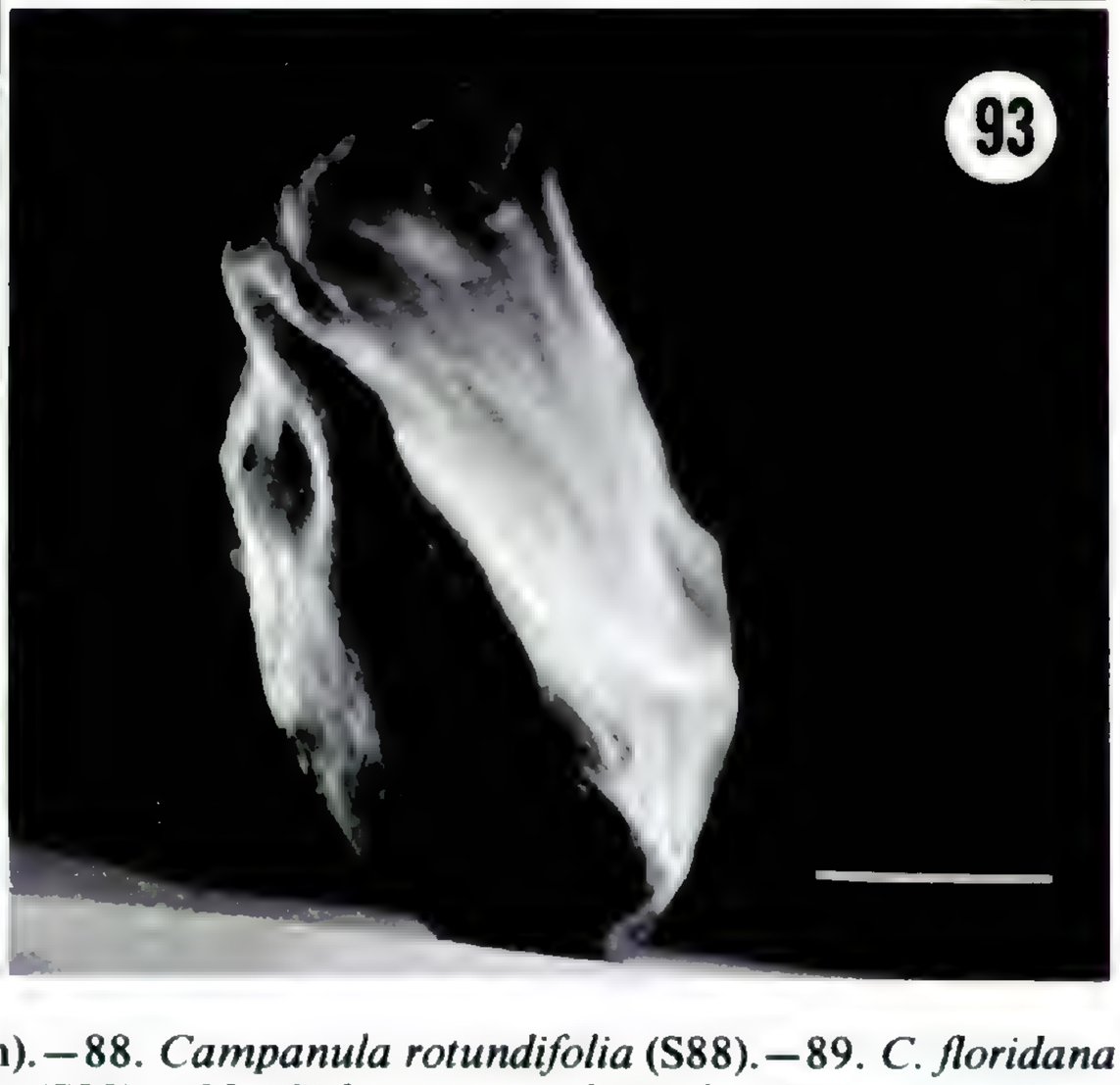
FIGURES 82–87 (bar = 100 μm). Seeds of *Legousia* and *Heterocodon*.—Figures 82, 83. *Legousia hybrida*.—82. Seed (S67).—83. Seed coat (S67).—Figures 84, 85. *Heterocodon rariflorum*.—84. Seed (S53).—85. Seed coat (S53).—Figures 86, 87. *Legousia pentagonia*.—86. Seed (S70).—87. Seed coat (S70).



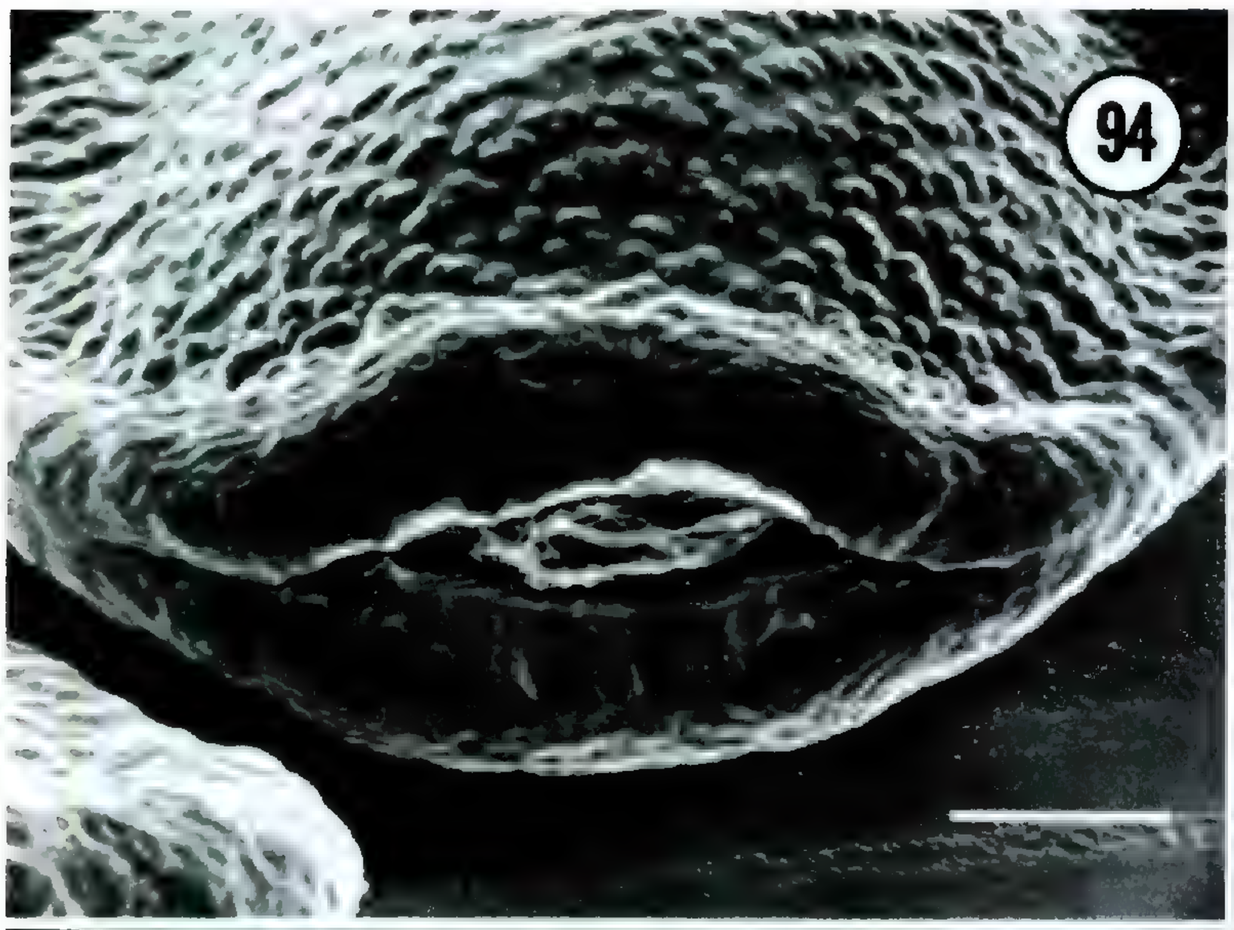


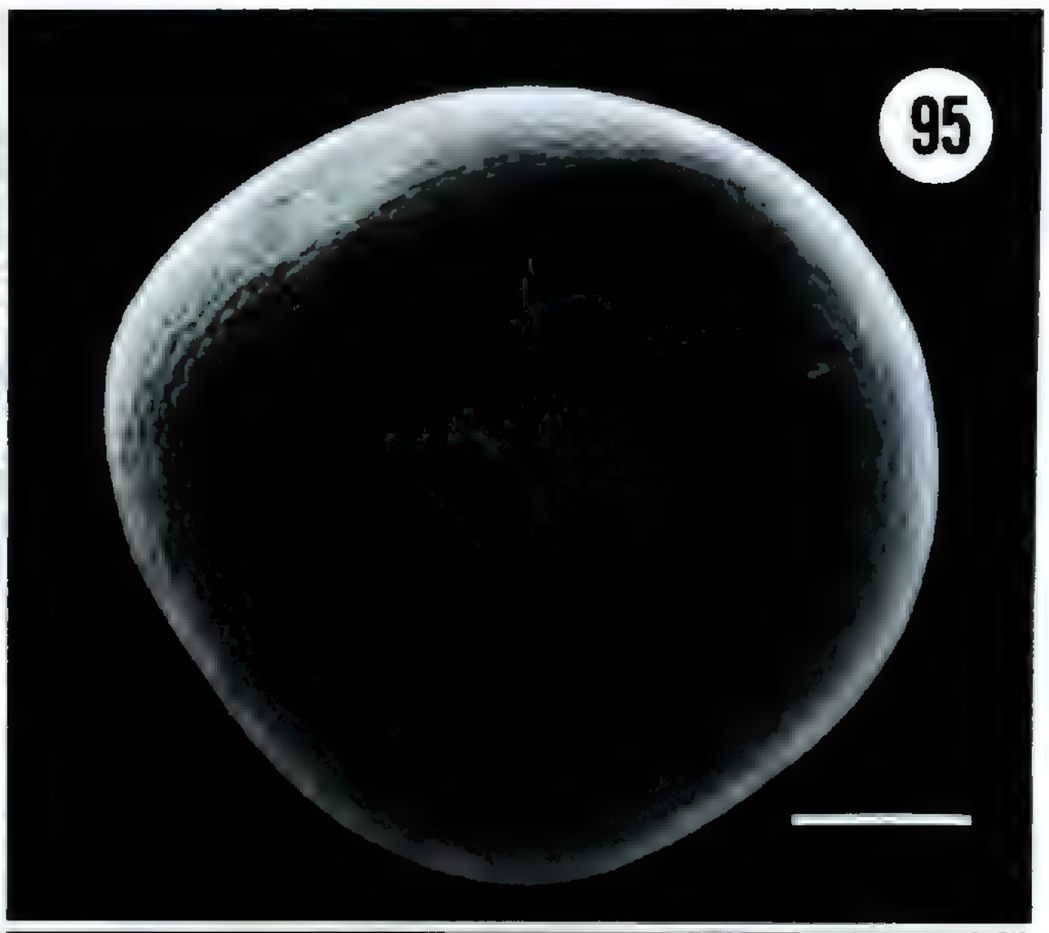


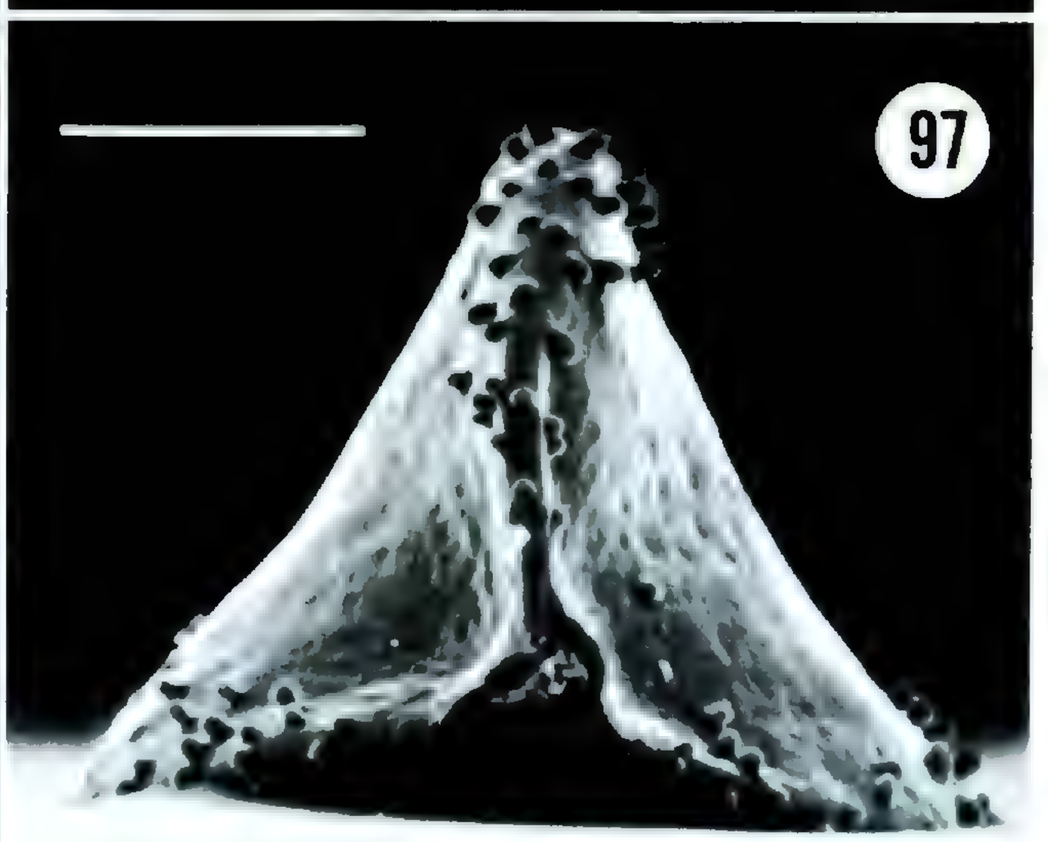


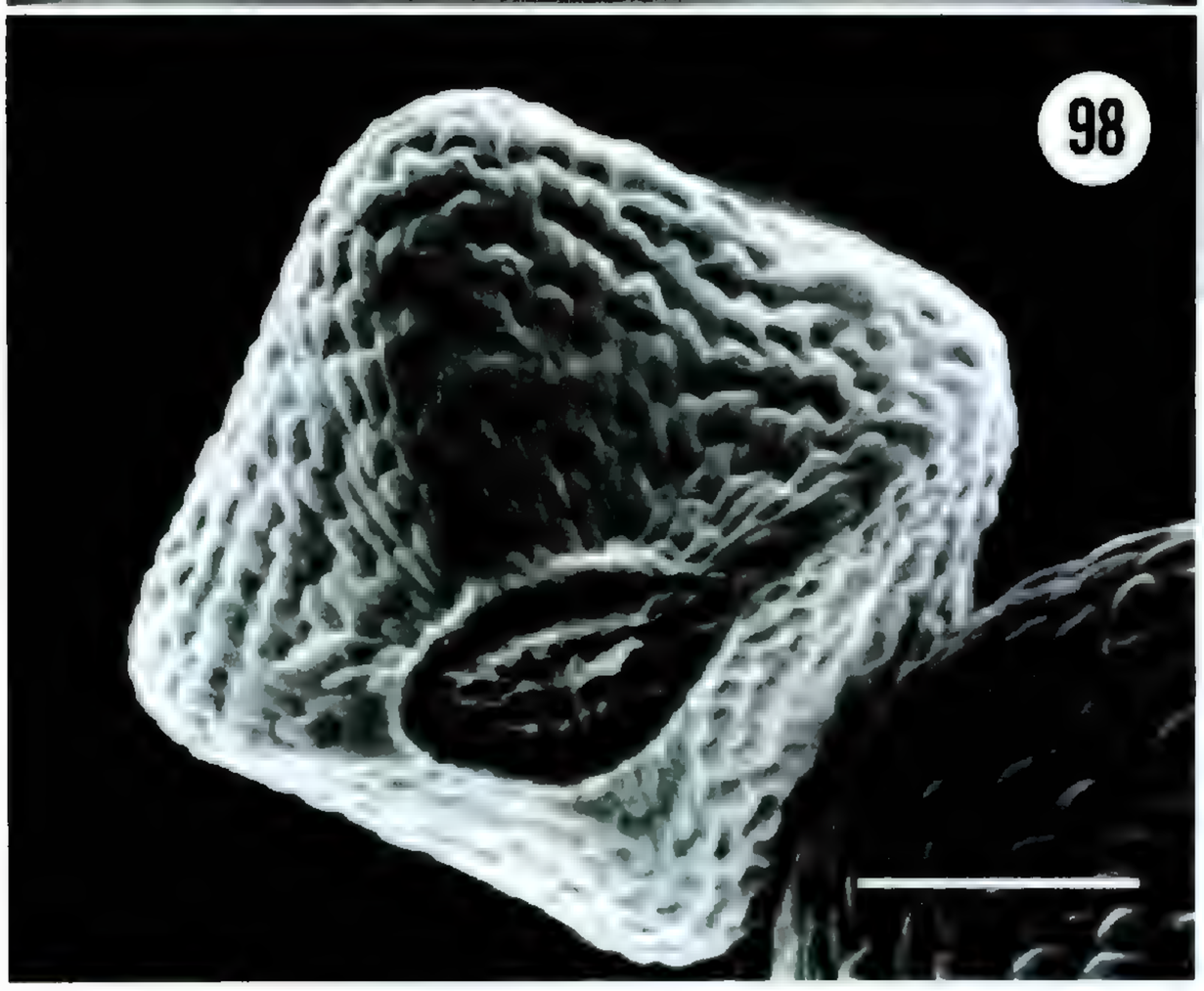


FIGURES 88–93. Face views of seeds (bar = 100 μm).—88. *Campanula rotundifolia* (S88).—89. *C. floridana* (S21).—90. *C. lasiocarpa* (S24).—91. *C. prenanthoides* (S08).—92. *Githopsis specularioides* (S76).—93. *Campanula exigua* (S64).

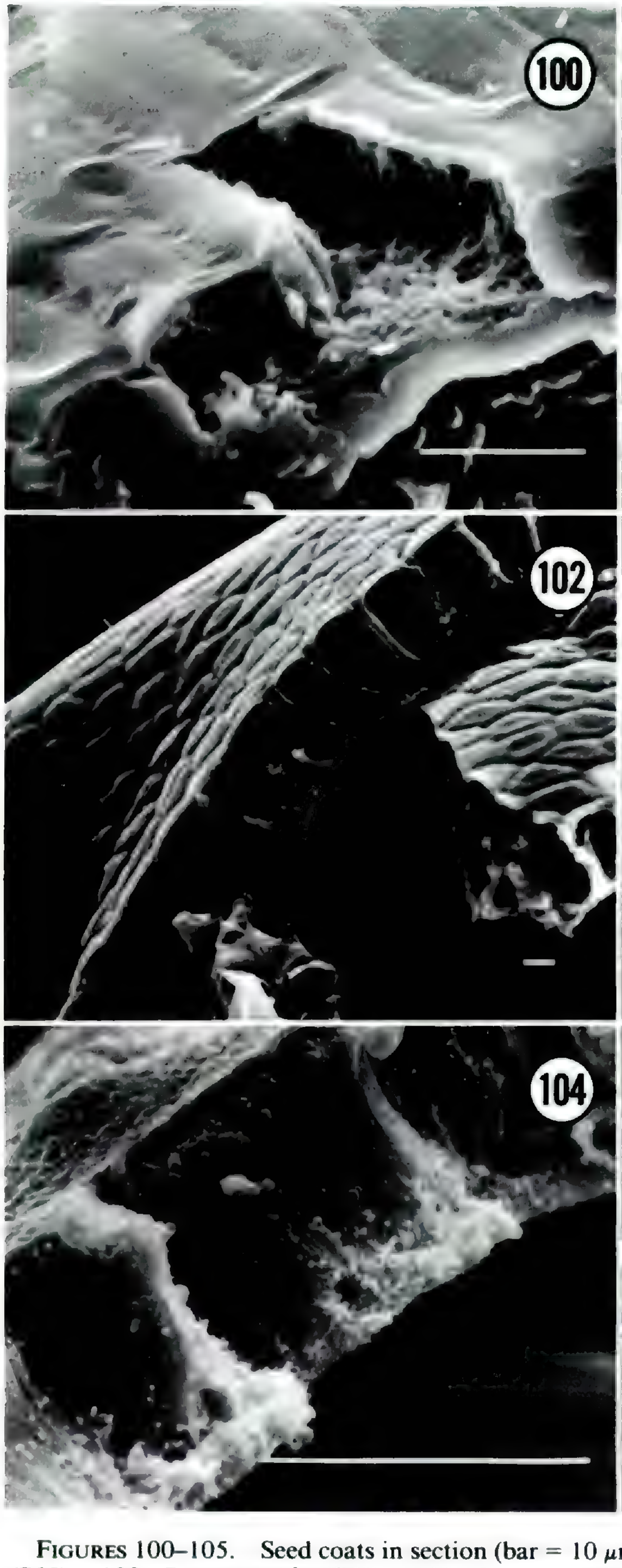


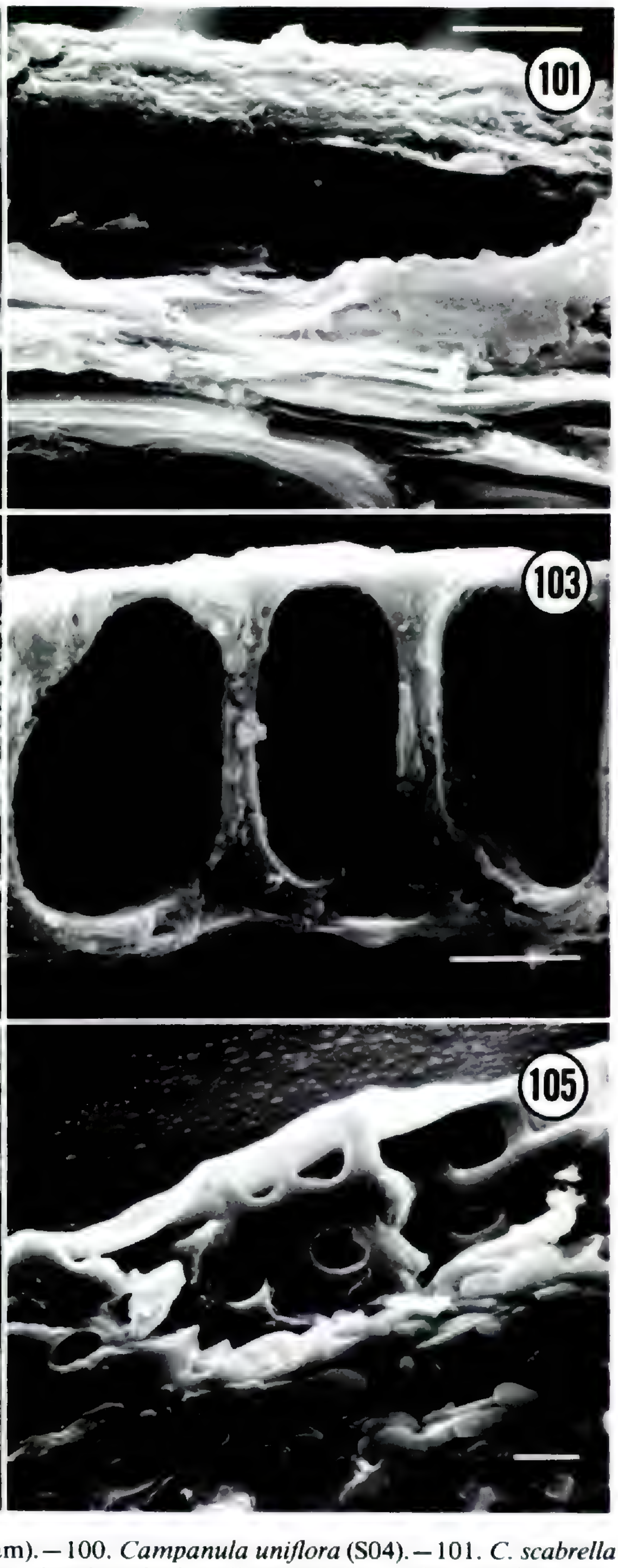




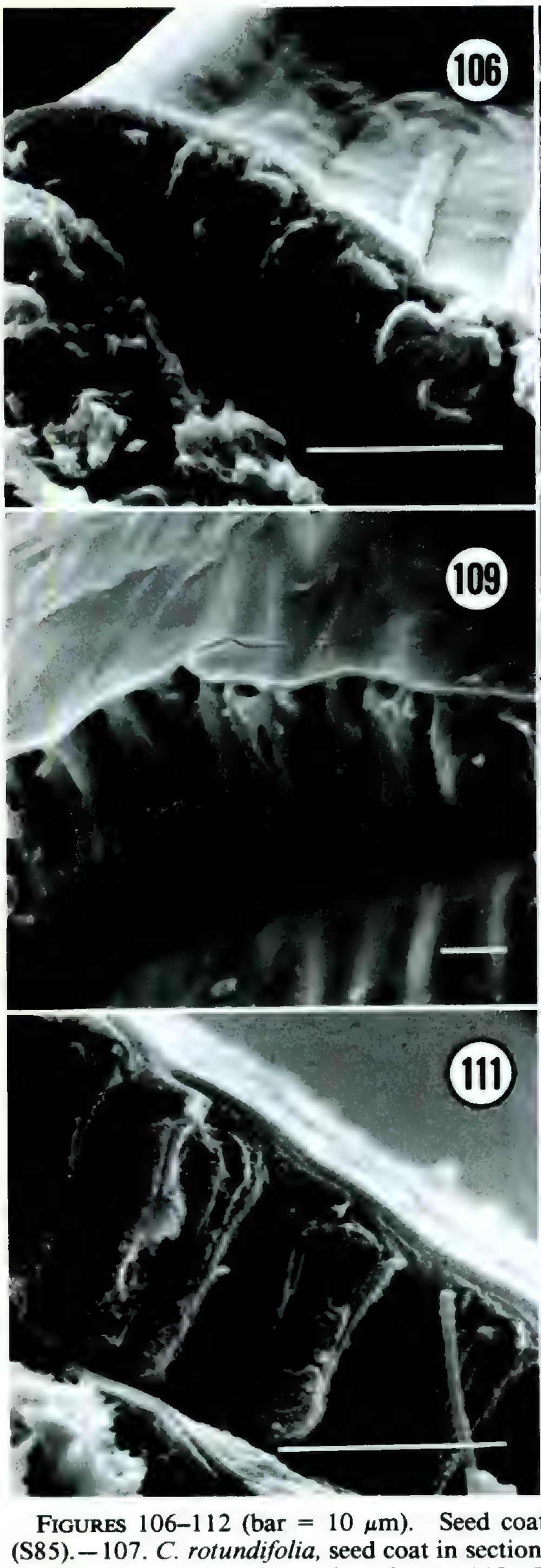


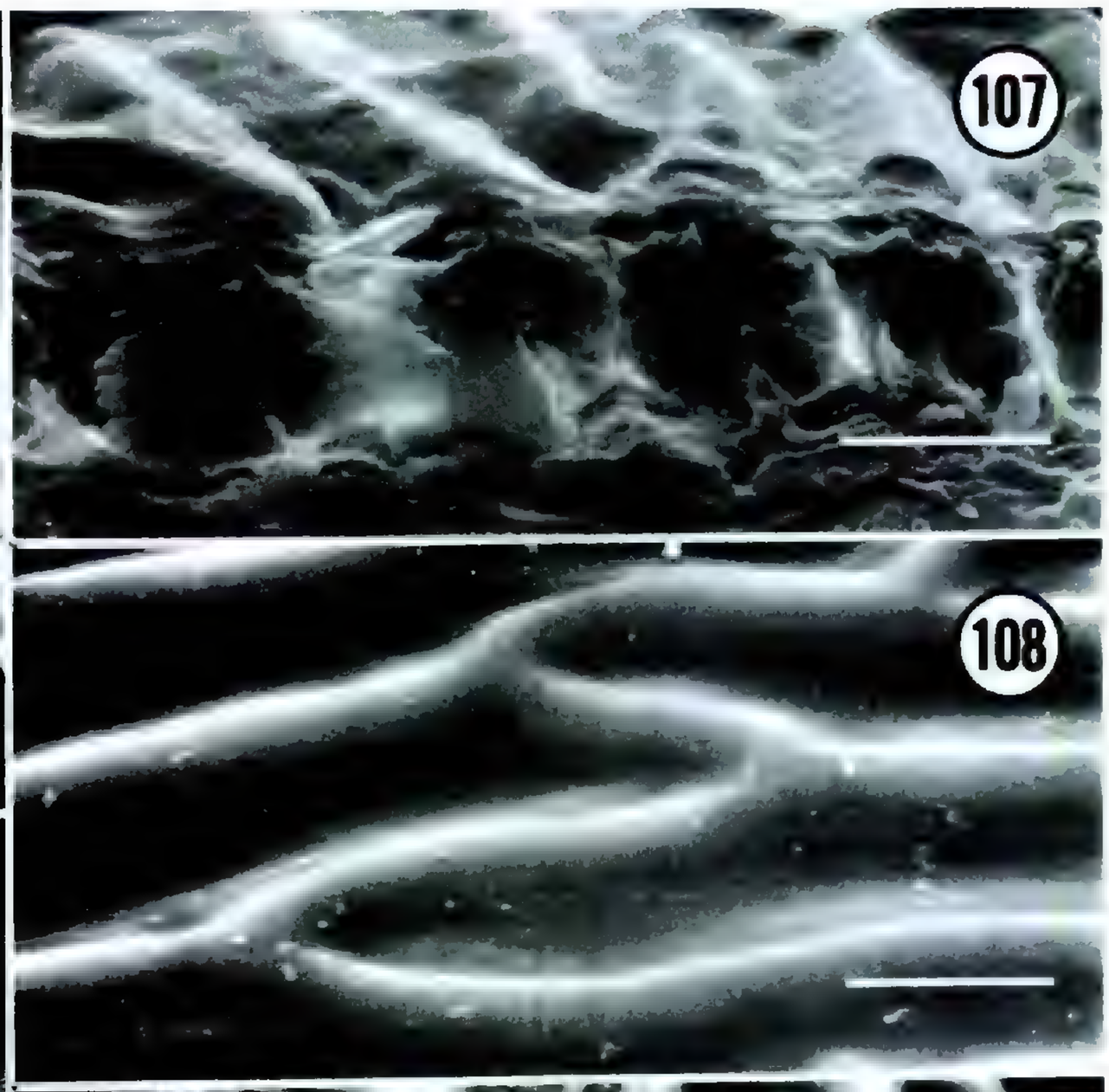
FIGURES 94–99. Face views of seeds (bar = 100 μm).—94. *Campanula americana* (S14).—95. *C. aparinoides* (S60).—96. *C. reverchoni* (S10).—97. *C. robinsiae* (S90).—98. *Triodanis texana* (S51).—99. *T. holzingeri* (S37).

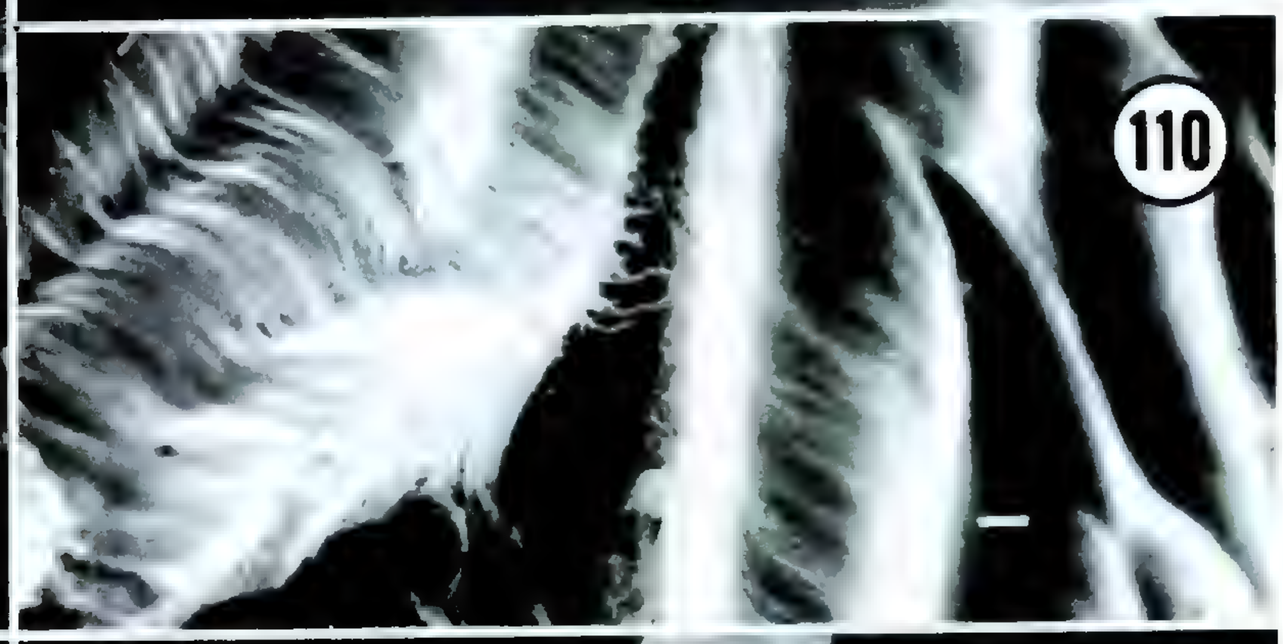


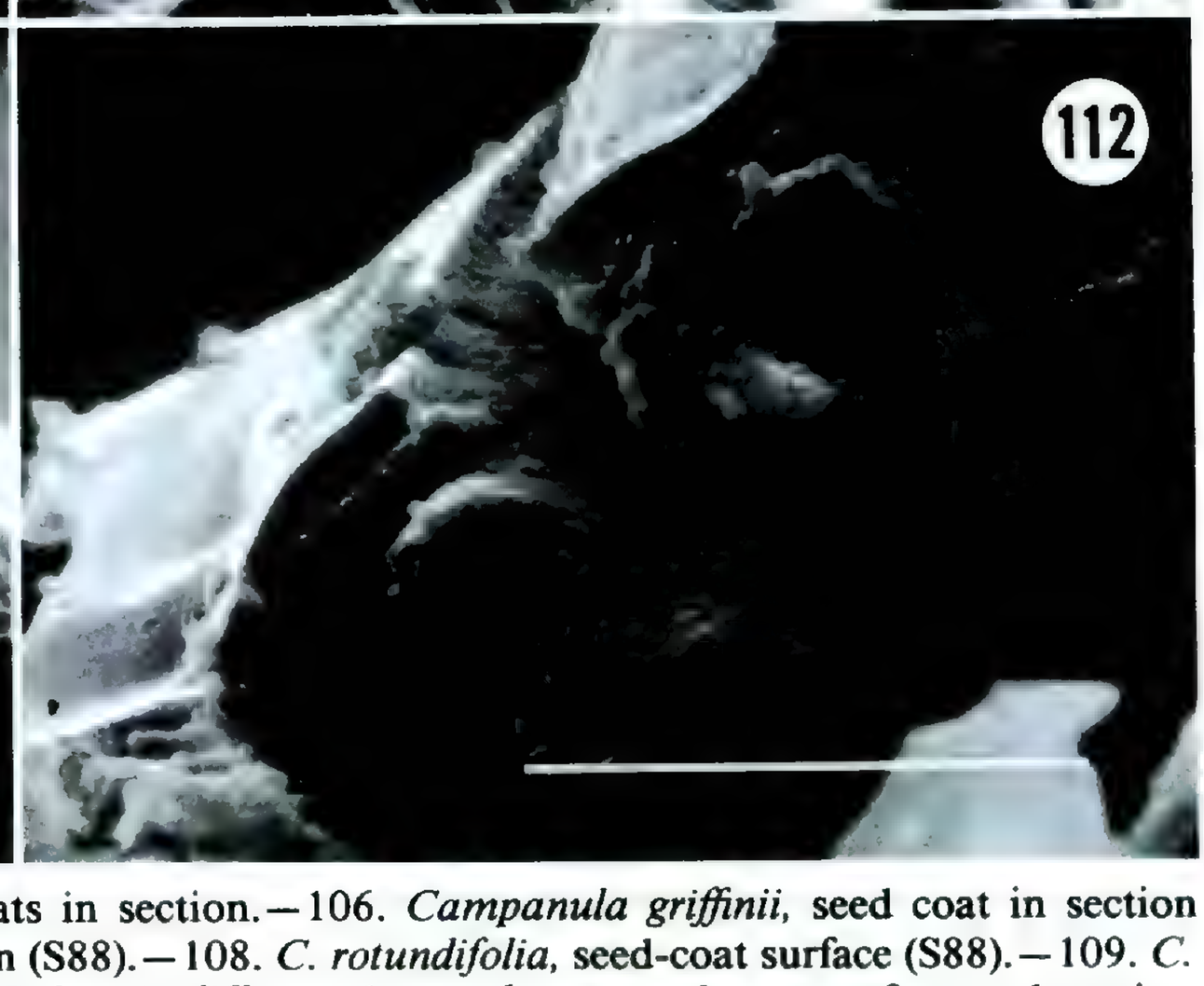


FIGURES 100–105. Seed coats in section (bar = 10 μm).—100. *Campanula uniflora* (S04).—101. *C. scabrella* (S65).—102. *C. aparinoides* (S61).—103. *C. aparinoides*, showing pits in cell walls (S63).—104. *Triodanis perfoliata* (S45).—105. *Campanula floridana*, showing wall pits (openings) (S21).

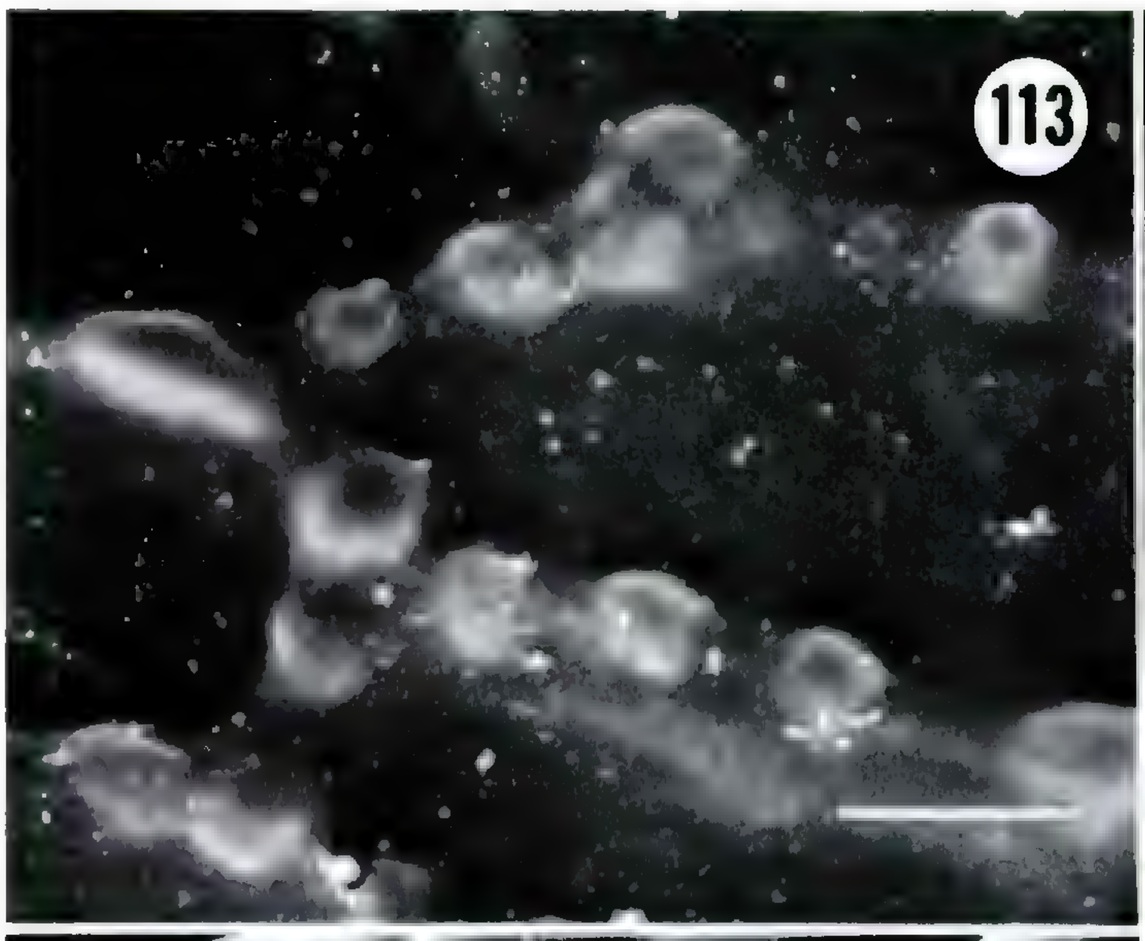


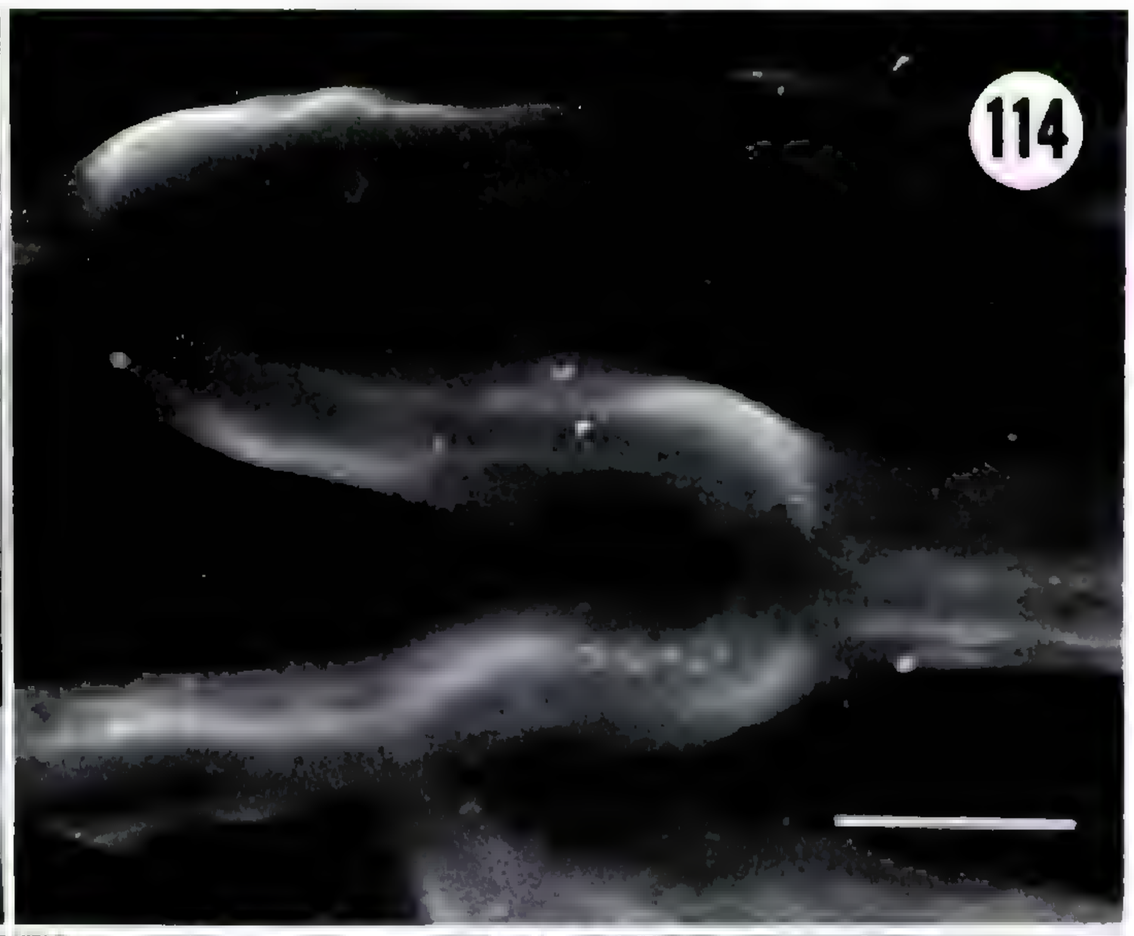


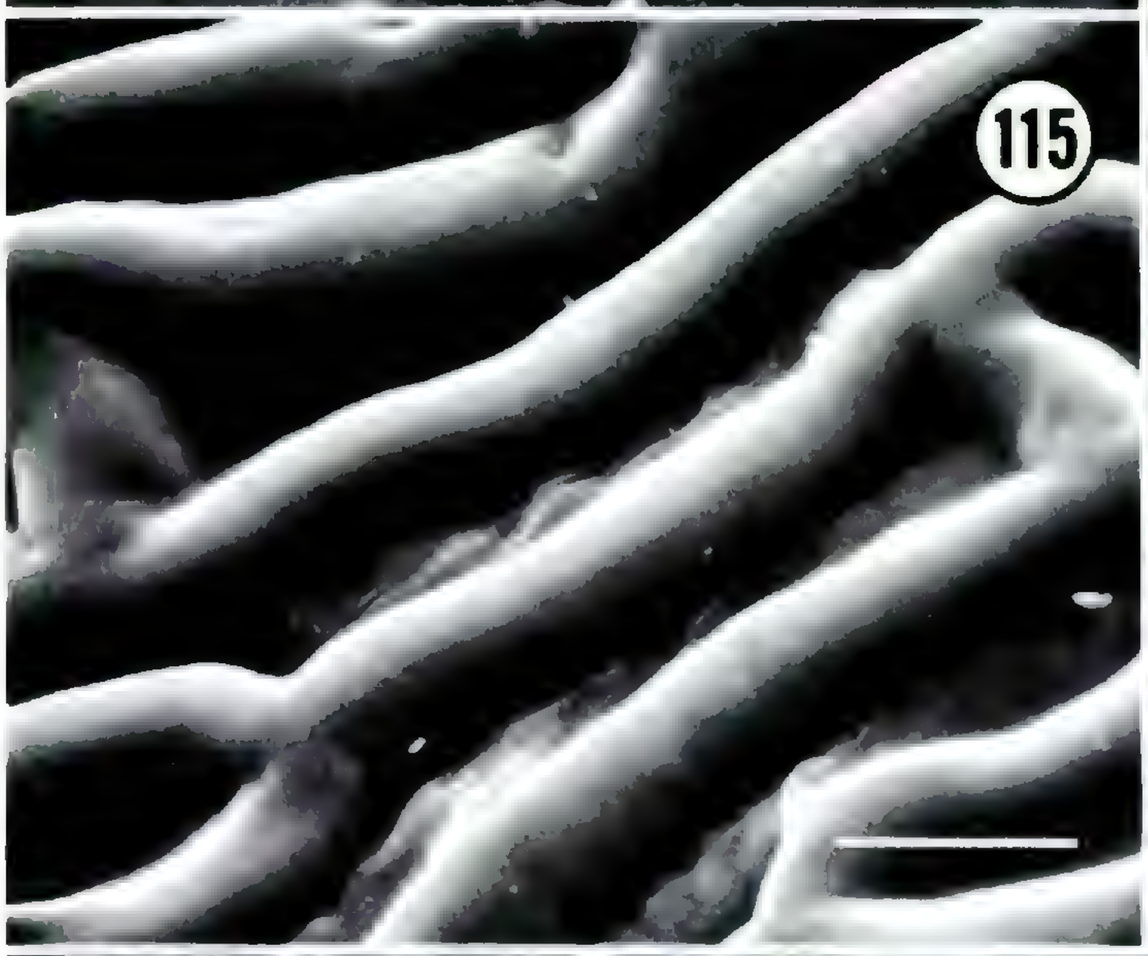


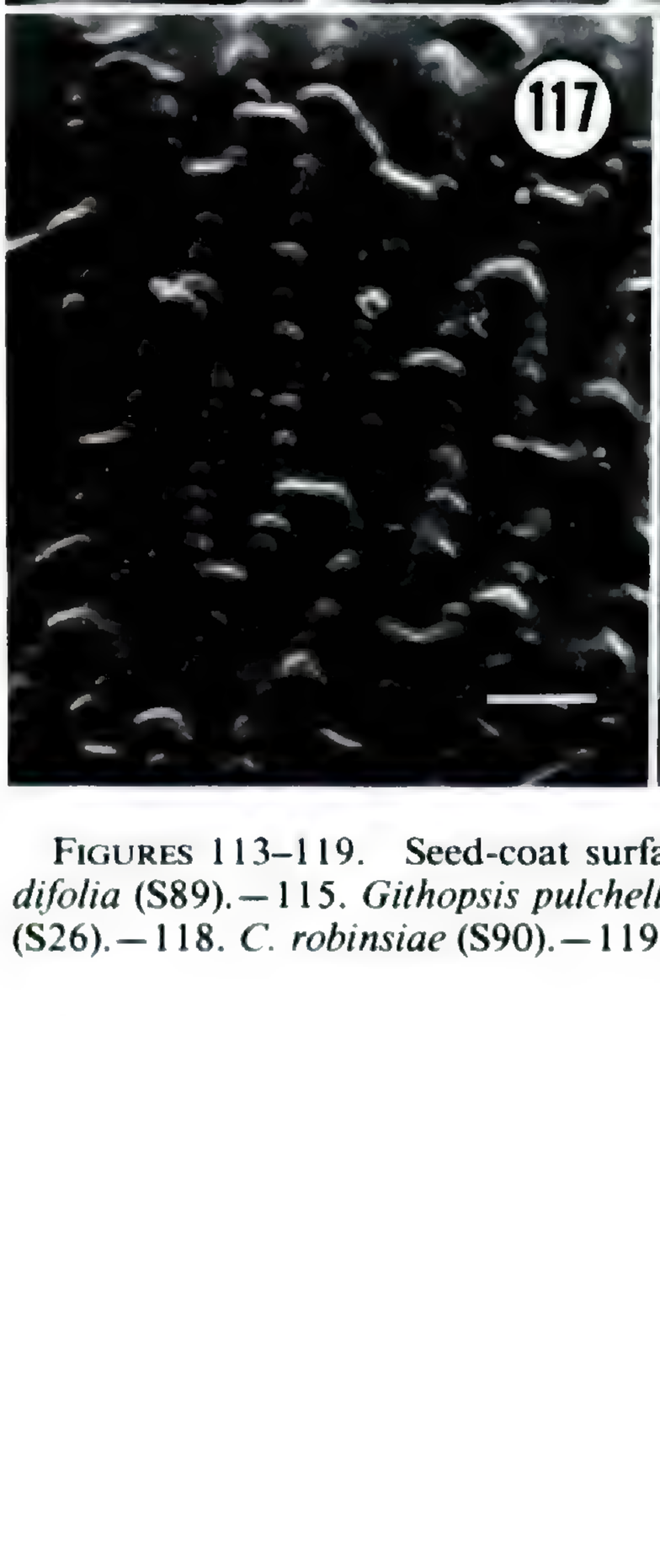


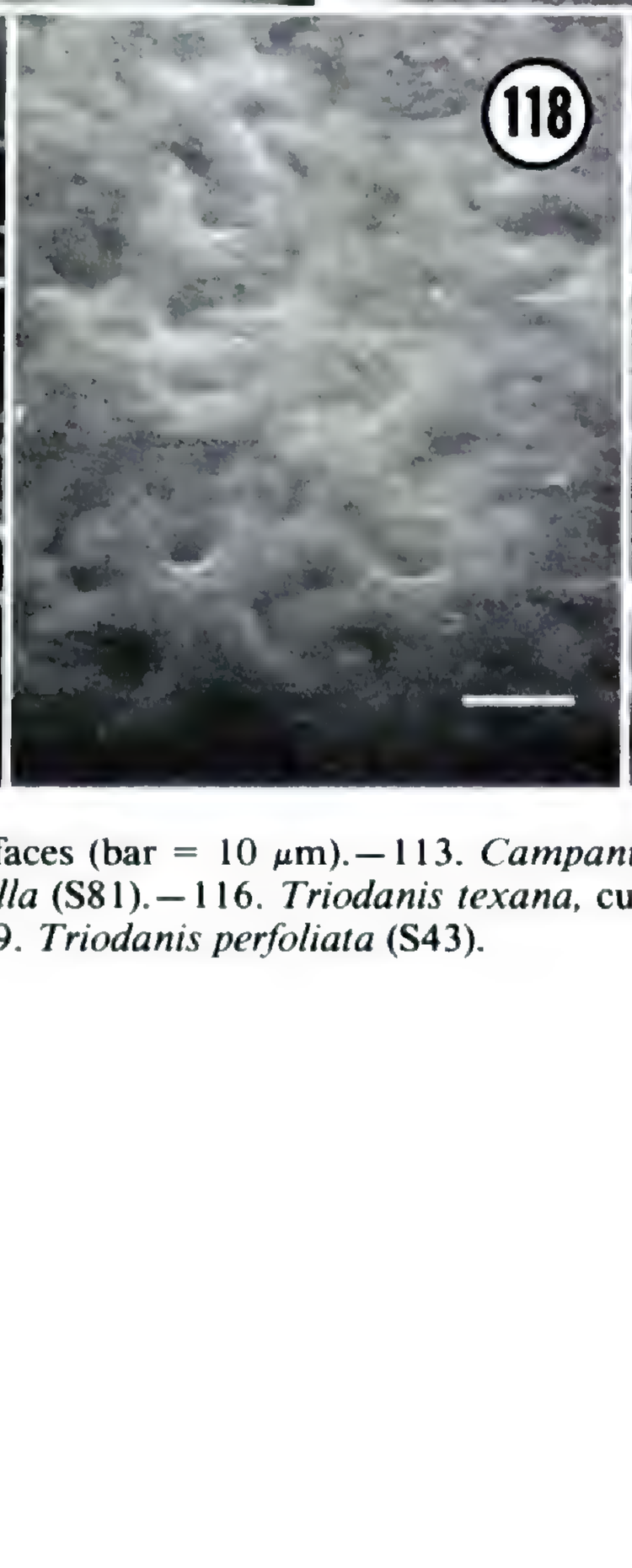
FIGURES 106–112 (bar = 10 μm). Seed coats in section.—106. *Campanula griffinii*, seed coat in section (S85).—107. *C. rotundifolia*, seed coat in section (S88).—108. *C. rotundifolia*, seed-coat surface (S88).—109. *C. californica*, seed coat in section (S17).—110. *Githopsis diffusa* subsp. *robusta*, seed-coat surface and section (S77).—111. *Legousia hybrida*, seed coat in section (S67).—112. *Triodanis biflora*, seed coat in section (S47).

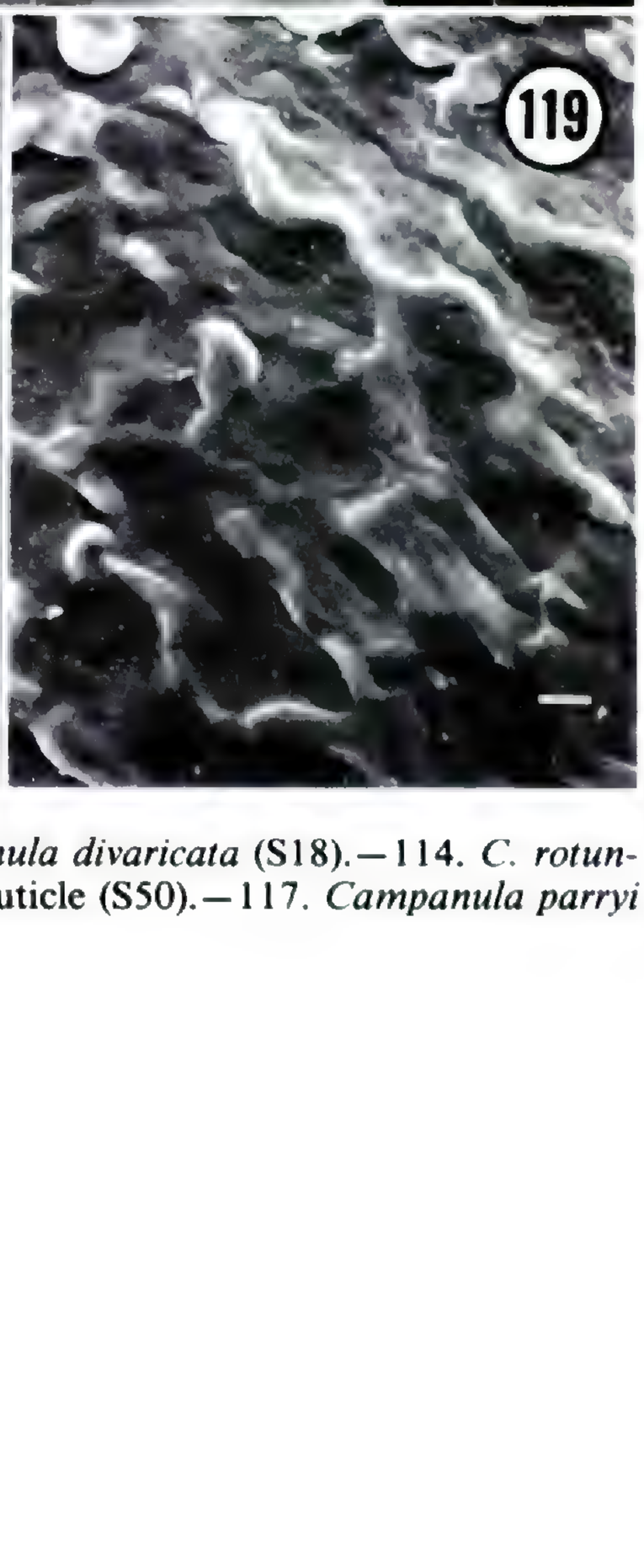












FIGURES 113–119. Seed-coat surfaces (bar = 10 μm).—113. *Campanula divaricata* (S18).—114. *C. rotundifolia* (S89).—115. *Githopsis pulchella* (S81).—116. *Triodanis texana*, cuticle (S50).—117. *Campanula parryi* (S26).—118. *C. robinsiae* (S90).—119. *Triodanis perfoliata* (S43).

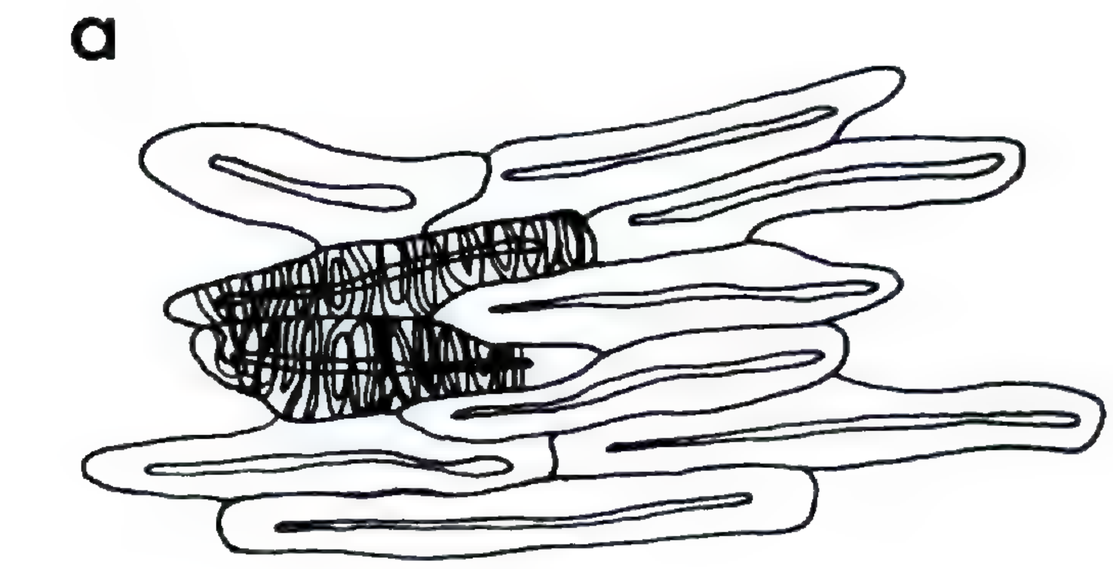


FIGURE 120. Camera lucida drawings of seed-coat peels (bar = 10 μm). Long axis of cells corresponds to long axis of the seed. Dark lines represent thickenings of radial walls; dots represent apparent pits on tangential walls.—a. *Campanula griffinii* (S85) (Type 1 pattern).—b. *C. divaricata* (S20) (Type 2 pattern).—c. *C. aparinoides* (S60) (Type 3 pattern).

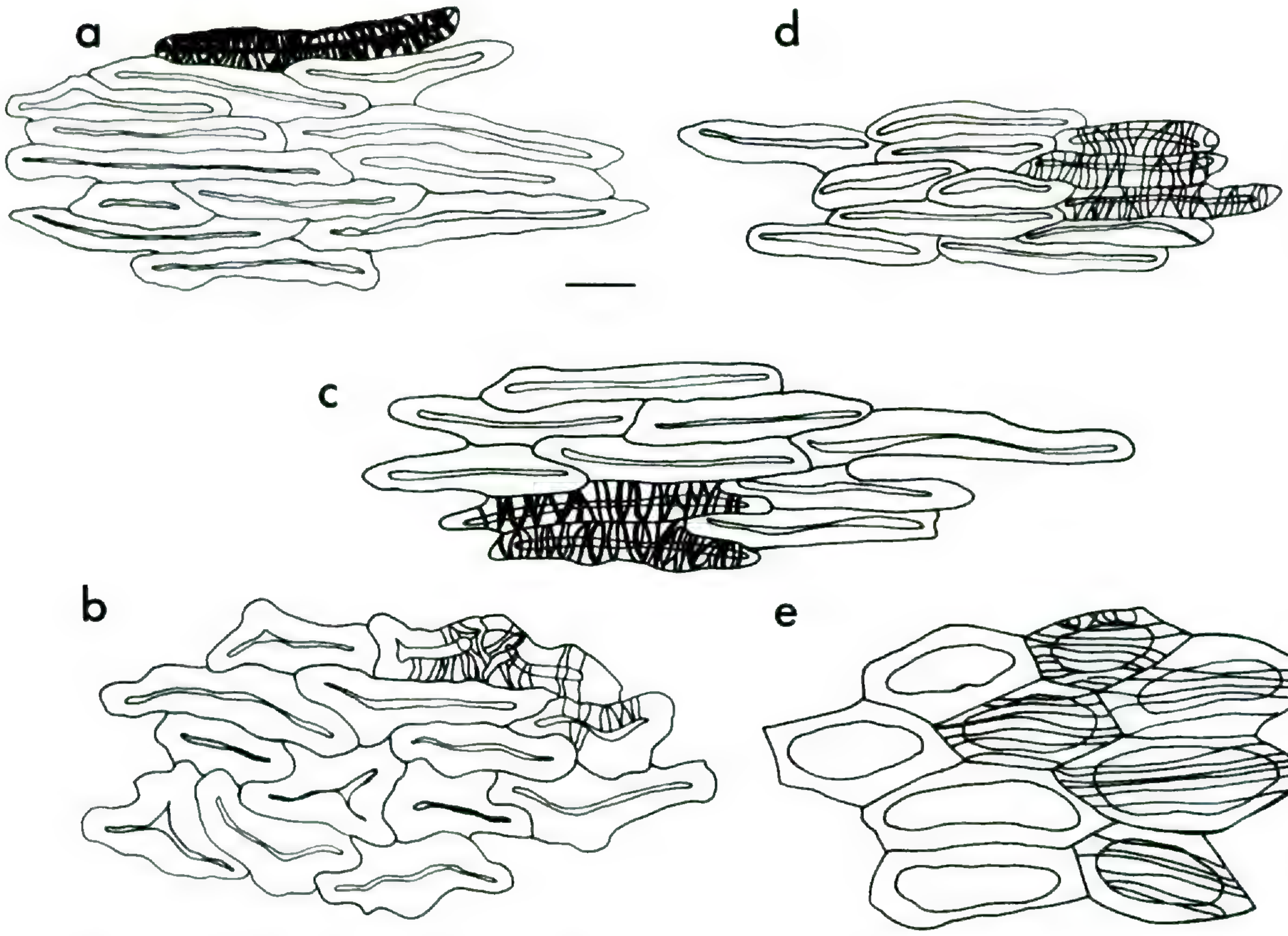


FIGURE 121. Camera lucida drawings of seed-coat peels (bar = 10 μm). Long axis of cells corresponds to long axis of the seed. Dark lines represent thickenings of radial walls.—a. *Campanula americana* (S15).—b. *Triodanis texana* (S49B).—c. *C. piperi* (S83).—d. *C. parryi* (S27).—e. *C. floridana* (S21).

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REVISION OF THE GUAYANA HIGHLAND BROMELIACEAE[1]

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ABSTRACT

Genera and species of Bromeliaceae that have been described from the Guayana Highland since *Flora Neotropica* treatments of the subfamilies Pitcairnioideae and Tillandsioideae by Smith and Downs in 1974 and 1977 are distinguished by amended or completely rewritten keys. Of the species, 26 are here described as new, 24 being Pitcairnioideae. *Lindmania* is resurrected from the synonymy of *Cottendorfia*, and an error in the validation of *Steyerbromelia* is corrected.

At the time of the monographs of the first two subfamilies of the Bromeliaceae in the *Flora Neotropica* (Smith & Downs, 1974, 1977), the area from which the most future additions were expected was the Guayana Highland. Recent collecting in the area has confirmed the suspicion. Among the new species added are 26 described in the present paper. In addition to the new species, mostly in the Pitcairnioideae, two Pitcairnioid genera, *Brewcaria* and *Steyerbromelia*, have been described (in Steyermark et al., 1984) since the *Flora Neotropica* monograph, and more recent studies have shown that Guayanian *Lindmania* must be resurrected from the synonymy of the genus *Cottendorfia* of eastern Brazil. The present paper, in addition to describing new species, summarizes by use of keys the distinctions of all species and genera described from the area since the monograph. Also, an error in the validation of *Steyerbromelia* is corrected.

The area covered in the present paper is the same as in the Bromeliaceae of the Guayana Highland (Smith, 1967), which should be referred to for a more complete presentation of the family in the area, especially in the subfamilies Tillandsioideae and Bromelioideae. The numbers preceding the species and genera follow those in the *Flora Neotropica*. New entries are given a decimal number under the number of the genus or species with which they would appear in the keys of the *Flora*. In view of the many additions, keys are provided to all known species of the Pitcairnioid genera, *Connellia, Lindmania, Steyerbromelia, Brocchinia,* and *Brewcaria,* and amended keys are provided for many parts of *Navia*.

PITCAIRNIOIDEAE

KEY TO GENERA

1a. Seeds appendaged.
  2a. Petal-blades tightly spiraled after anthesis; ovary superior or slightly inferior. Andean plants of open slopes and summits from Costa Rica and Guyana to Chile and Argentina ..... 1. *Puya*
  2b. Petal-blades remaining separate after anthesis.
    3a. Ovary wholly superior; ovules bicaudate; petals regular.
      4a. Sepals convolute with the left side of each overlapping the right of the next one; petals naked; inflorescence simple or compound. Guayana Highland.
        5a. Anthers subbasifixed; petals brightly colored, more or less massed together after anthesis but not twisted; sepals large and firm ..... 4. *Connellia* (p. 690)
        5b. Anthers equitant; petals white or rose, separate after anthesis; sepals not over 10 mm long, thin at least marginally ..... 5. *Lindmania* (p. 690)
      4b. Sepals imbricate; petals appendaged with 2 vertically attached scales; inflorescence compound ..... 5a. *Steyerbromelia* (p. 699)
    3b. Ovary partially to wholly inferior.
      6a. Sepals convolute with the left side of each overlapping the right of the next one; petals large, usually zygomorphic and forming a hood over the anthers. Mexico and the West Indies to Argentina and Brazil ..... 8. *Pitcairnia* (p. 700)

[1] In this paper the new species are coauthored by Julian Steyermark, who collected and made initial observations of most of the specimens, and in the Pitcairnioideae by Harold Robinson who provided the anatomical observations. Careful editing of the manuscript by Robert Read is greatly appreciated.

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6b. Sepals imbricate with both posterior ones overlapping the anterior; petals small, regular. Guayana Highland.
7a. Epigynous tube lacking; inflorescence open and definitely branched ..... 9. *Brocchinia* (p. 702)
7b. Epigynous tube well developed; inflorescence sessile, capitate ..... 10. *Ayensua*
1b. Seeds naked or with a very narrow circumferential wing; sepals imbricate. Guayana Highland.
8a. Petals naked; inflorescence usually compound or densely capitate ..... 11. *Navia* (p. 703)
8b. Petals appendaged with 2 horizontally attached scales; inflorescence simple, densely cylindric ..... 11a. *Brewcaria* (p. 714)

4. **CONNELLIA** N. E. Brown, Trans. Linn. Soc. II. 6: 66, pl. 13. 1901.

1a. Inflorescence compound although the short branches often covered by ample primary bracts at anthesis.
2a. Sepals ecarinate, 12 mm long; branches not elongating in fruit. Roraima ..... 2. *C. augustae*
2b. Sepals sharply carinate, 14–21 mm long; branches greatly elongating in fruit.
3a. Leaf-blades concolorous, serrate at base; inflorescence glabrous; sepals elliptic, obtuse, 14 mm long. Ptari-tepui, Cerro Venamo ..... 1. *C. nutans*
3b. Leaf-blades narrowly pale-margined, serrulate throughout; inflorescence villose or villosulous; sepals lanceolate, acuminate, 21 mm long. Auyan-tepui ..... 1.1. *C. varadarajanii*
1b. Inflorescence simple.
4a. Leaf-blades densely tomentose-lepidote above and on the margins. Roraima ..... 3. *C. quelchii*
4b. Leaf-blades glabrous above, green with prominent white margins. Ilu-tepui, Gran Sabana ..... 4. *C. caricifolia*

1.1. *Connellia varadarajanii* L. B. Smith & Steyermark, Journ. Bromel. Soc. 35: 52, fig. 2. 1985 (fig. 1 was actually *C. smithiana* Steyermark & Luteyn).

The leaf anatomy of the recently described species has been examined to allow comparison with other members of the genus. The vascular bundles are recessed in chlorenchyma adaxially but exposed to water storage tissue, they are narrowly covered by chlorenchyma abaxially; water storage cells 3–4-stratose adaxially, ca. 3-stratose in distinct canals abaxially; subepidermal cells with one subdistinct layer adaxially with outer walls slightly thickened, with one distinct moderately thickened layer abaxially; substomatal pore not occluded, oval or rounded; abaxial surface with minute subpeltate or shortly strap-shaped scales, cells transversely oblong.

The leaf cross-section shows the pattern of some water storage tissue and a narrow layer of chlorenchyma abaxial to the vascular bundles similar to the pattern in the four species of *Connellia* known at the time of the anatomical study of Robinson (1969). Of the four, only *C. quelchii* has larger bundles lacking abaxial chlorenchyma. None of the other species has as much abaxial water storage tissue, but *C. nutans* seems closest in this regard. *Connellia nutans* and *C. augustae* do not have the vascular bundles recessed in the chlorenchyma adaxially as in the new species, *C. quelchii,* and *C. caricifolia.*

The general form of the leaf cross-section is the type seen again in such species of *Lindmania* as *L. brachyphylla, L. tillandsioides, L. riparia* and *L. sessilis,* and the genus *Connellia* may relate to that element of *Lindmania.*

The general type of leaf cross-section seen in *Connellia* is not found in the recently described *C. smithiana* in which the larger vascular bundles all have fiber sheaths continuous with the abaxial epidermis. This reenforces other evidence that *C. smithiana* should be transferred from *Connellia* to *Lindmania.* The abaxially buttressed bundles are similar to those seen in *Lindmania minor, L. thyrsoidea,* and the newly described *L. huberi* and *L. imitans.*

2. *Connellia augustae* N. E. Brown is endemic to Roraima. Other citations in Fl. Neotrop. no. 14(1): 211, 1974, are *C. nutans* L. B. Smith.

5.2. **LINDMANIA** Mez, DC. Monogr. Phan. 9: 535. 1896.

The resurrection of the Guayanian *Lindmania* comes as a result of further study that puts greater emphasis on the aestivation or overlapping of the sepals. There have been two previous indications of generic difference noted between *Lindmania* and the Bahian *Cottendorfia* to which I had reduced it (Smith & Downs, 1974: 212). Robinson (1969: 8) pointed out significant differences in the cell walls of the abaxial epidermis and in the stomata. Recently I verified by specimens the unisexual nature of the flowers in *Cot-*

tendorfia. Mez (1894, pl. 93) had illustrated it as unisexual although he described the genus as having "Flores hermaphroditi" (p. 502). Finally, I now find that the sepals of *Lindmania* are convolute with the left side of each overlapping the right of the next one while those of *Cottendorfia* are cochlear with the anterior sepal overlapping the two posterior ones.

The following key, although still largely artificial, eliminates weak points in that of the *Flora Neotropica* but keeps its enumeration. Robinson's findings are included and in some cases show correlation with the macroscopic characters.

1a. Inflorescence simple or subsimple.
2a. Scape very short or lacking; inflorescence dense, hidden in the leaves. Chimantá.
3a. Leaf-blades straight; sepals broadly lanceolate, 9 mm long ..... 24. *L. navioides*
3b. Leaf-blades strongly recurved; sepals suborbicular, 4 mm long ..... 24.1. *L. huberi*
2b. Scape evident; inflorescence lax or sublax.
4a. Flowers in fascicles; inflorescence otherwise very lax. Chimantá ..... 20. *L. subsimplex*
4b. Flowers single.
5a. Scape-bracts much shorter than the internodes; scape slender (inflorescence normally bipinnate). Northwestern Guyana and adjacent Venezuela ..... 15. *L. guianensis*
5b. Scape-bracts exceeding the internodes.
6a. Plant arachnoid-vestite; scape relatively stout, 4 mm thick, to 36 cm long. Marahuaca ..... 20.1. *L. arachnoidea*
6b. Plant obscurely lepidote; scape 1.5 mm thick, to 10 cm long. Chimantá.
7a. Scape-bracts very narrow, completely exposing the scape; leaf-blades 5 mm wide ..... 20.2. *L. aurea*
7b. Scape-bracts ample, densely imbricate; leaf-blades 10 mm wide ..... 20.3. *L. imitans*
1b. Inflorescence bipinnate or rarely subtripinnate or subsimple with a distinct basal branch.
8a. Primary bracts equaling or exceeding the sterile bases of at least the lower branches.
9a. Floral bracts about equaling to exceeding the pedicels.
10a. Pedicels 8 mm long; inflorescence tomentose-lepidote. Neblina ..... 16. *L. maguirei*
10b. Pedicels not more than 3.5 mm long or lacking.
11a. Branches 1.5–4 cm long, inflorescence narrowly cylindric, at least at apex.
12a. Floral bracts narrowly triangular; leaf-blades entire, much exceeding the inflorescence; 1 cm wide. Chimantá ..... 22. *L. stenophylla*
12b. Floral bracts lanceolate to broadly elliptic; leaf blades toothed near the base or not much exceeding the inflorescence.
13a. Inflorescence dense only near apex; scape-bracts shorter than the upper internodes; leaf blades entire, ca. 1 cm wide. Abácapa-tepui ..... 19. *L. tillandsioides*
13b. Inflorescence dense throughout; scape-bracts densely imbricate; leaf blades minutely toothed basally, 35 mm wide. Auyan-tepui ..... 19.1. *L. riparia*
11b. Branches more than 4 cm long, divergent; inflorescence lax or sublax.
14a. Flowers 3–3.5 mm pedicellate.
15a. Inflorescence subdensely vestite with microscopic glanduliform ferruginous scales; primary bracts entire; leaf-blades serrulate only at base. Cerro Parú ..... 11. *L. phelpsiae*
15b. Inflorescence flocculose with fine linear white scales; primary bracts serrulate; leaf-blades serrulate throughout. Apacará-tepui, Chimantá ..... 2. *L. serrulata*
14b. Flowers sessile. Chimantá.
16a. Leaf-blades serrulate, 35 mm wide; plant flowering over 7 dm high ..... 2.1. *L. sessilis*
16b. Leaf-blades entire, 12 mm wide; plant flowering 46 cm high ..... 2.2. *L. saxicola*
9b. Floral bracts distinctly shorter than the pedicels.
17a. Sterile base longer than the fertile part of branch, about equaling primary bract. Auyan-tepui ..... 13. *L. longipes*
17b. Sterile base shorter than fertile part of branch, much shorter than the basal primary bracts.
18a. Inflorescence lateral in leaf-axils, subtripinnate. Neblina ..... 4.1. *L. lateralis*
18b. Inflorescences terminal; primary bracts equaling or shorter than the branches.
19a. Branches short; inflorescence densely cylindric.

20a. Primary bracts very narrow, wholly exposing the branches; inflorescence erect. Serrania Yutaje ..... 21. *L. thyrsoidea*
20b. Primary bracts broad, covering most of each branch; inflorescence prostrate. Auyan-tepui ..... 21.1. *L. smithiana*
19b. Branches elongate; inflorescence lax at least at base.
21a. Pedicels subfiliform, spreading, about as long as the flowers.
22a. Inflorescence glabrous; pedicels 10–15 mm long; leaf-blades laxly serrate throughout. Duida, Abacapá-tepui, Marahuaca ..... 4. *L. wurdackii*
22b. Inflorescence vestite; pedicels 3.5–7 mm long.
23a. Pedicels 3.5 mm long; inflorescence vestite with pale narrow spreading scales. Cerro Venamo, Gran Savanna ..... 3. *L. gracillima*
23b. Pedicels 7 mm long; inflorescence tomentulose-lepidote, verruculose. Neblina ..... 12. *L. dendritica*
21b. Pedicels cylindric or obconic, longer than the flowers.
24a. Leaf-blades densely flocculose beneath, obscurely denticulate throughout; inflorescence flocculose. Chimantá ..... 23. *L. minor*
24b. Leaf-blades glabrescent, serrulate at base.
25a. Inflorescence vestite; scape and primary bracts with distinct ovate base and long very narrow blade. Serra Aracá ..... 23.1. *L. piresii*
25b. Inflorescence glabrous; scape and primary bracts narrowly triangular with little distinction between base and blade. Marahuaca.
26a. Leaf-blades verruculose; flowering shoot obviously very tall (ca. 2 m estimate) and straight ..... 23.2. *L. terramarae*
26b. Leaf-blades smooth except for nerves; flowering shoot to 1 m tall and decurving ..... 23.3. *L. marahuacae*

8b. Primary bracts all shorter than the sterile bases of the branches.
27a. Floral bracts exceeding the pedicels.
28a. Leaf-blades linear-lanceolate with slightly convex sides, 33 mm wide, plane or narrowly revolute. Sarven-tepui, Auyan-tepui ..... 17. *L. brachyphylla*
28b. Leaf-blades narrowly triangular with straight sides, 15 mm wide, strongly involute. Chimantá ..... 18. *L. steyermarkii*
27b. Floral bracts about equaling or shorter than the pedicels.
29a. Scape-bracts much shorter than all but the lowest internodes.
30a. Leaf-blades serrulate toward base; margins recurved; axis 5 mm thick; racemes dense. Western Venezuela and adjacent Guyana and Brazil ..... 14. *L. geniculata*
30b. Leaf-blades entire; margins incurved; axis 2.5 mm thick; racemes lax. Roraima, Kaieteur Plateau, Gran Savanna ..... 15. *L. guianensis*
29b. Scape-bracts exceeding all or all but the highest internodes.
31a. Indument on the upper side of the leaf-blade; inflorescence glabrous; leaf-margins recurved. Central Guayana Highland ..... 5. *L. paludosa*
31b. Indument mostly or wholly on the underside of the leaf-blade; inflorescence glabrous or vestite.
32a. Racemes lax; leaf-blades 15 mm wide. Central Guayana Highland ..... 10. *L. argentea*
32b. Racemes dense or subdense; leaf blades 24–40 mm wide.
33a. Pedicels 5–12 mm long, much exceeding the floral bracts; leaf-margins recurved.
34a. Sepals retuse, verruculose; leaf-blades 40 mm wide, their indument persistent; pedicels 5 mm long. Serrania Yutaje ..... 6. *L. cylindrostachya*
34b. Sepals broadly elliptic, even; leaf-blades largely glabrescent, 25–35 mm wide.
35a. Branches curved ascending. Neblina ..... 7. *L. savannensis*
35b. Branches straight, spreading. Cerro Guaiquinima ..... 7.1. *L. atrorosea*
33b. Pedicels 1.5–3 mm long, about equaling the floral bracts.
36a. Sterile bases of the branches to 7 cm long, about twice the length of the primary bracts. Neblina ..... 8. *L. nubigena*
36b. Sterile bases of the branches not over 2 cm long, only slightly exceeding the primary bracts. Auyan-tepui ..... 9. *L. dyckioides*

2. *Lindmania serrulata* L. B. Smith, Contr. U.S. Nat. Herb. 29: 283, fig. 8. 1949. *Cottendorfia serrulata* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.

2b. *Lindmania serrulata* var. *reducta* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 414. 1957. *Cottendorfia serrulata* var. *reducta* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.

2.1. **Lindmania sessilis** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 1, 27a–d. TYPE: Venezuela. Bolívar: Distrito Piar, Macizo del Chimantá, Sector centro-noreste del Chimantá-tepui, cabeceras orientales del Caño Chimantá, ca. 2,000 m alt., Lat. 5°18′N, Long. 62°09′W, 26–29 Enero 1983, *Julian A. Steyermark, Otto Huber & Victor Carreño E. 128104* (holotype, US; isotype, VEN).

Planta e fragmentis perveteribus solum cognita, florigera ultra 7 dm alta. Folia 5 dm longa; vaginis brevibus amplis; laminis anguste triangularibus, 35 mm latis, omnino serrulatis, ad basim subtus dissite lepidotis.

Scapus rectus, ca. 15 mm diametro; scapi bracteis erectis, subfoliaceis, internodia multo superantibus. Inflorescentia laxe bipinnatim paniculata, setifera; bracteis primariis eis scapi similibus, ramorum basibus sterilibus brevissimis longioribus; ramis rectis, divergentibus, ad 11 cm longis, dense florigeris. Bracteae florigerae anguste triangulares, serrulatae, sepala superantes; floribus sessilibus. Sepala ovata, ca. 5 mm longa, base setifera. Capsula ovoidea; seminibus bicaudatis.

Leaf anatomy. Vascular bundles not or little recessed in chlorenchyma and exposed to water storage tissue adaxially, narrowly covered by chlorenchyma abaxially; water storage cells 3–4-stratose adaxially, in distinct canals with firm-walled cells abaxially, subepidermal cells adaxially and abaxially bistratose, smaller cells thickened on the exterior part of their walls; substomatal pores small, oval, with walls subincrassate; abaxial scales small, peltate, with cells of the disk indistinct.

This leaf anatomy is seen also in *Lindmania* in *L. tillandsioides, L. brachyphylla,* and the newly described *L. riparia,* and it is probably most closely related to these in spite of the shorter primary bracts or longer and laxer branching of the inflorescence that separate the species in the key. The new species seems to have the vascular bundles adaxially less recessed in the chlorenchyma than the other species.

Known only from the type.

2.2. **Lindmania saxicola** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 2, 27e–h. TYPE: Venezuela. Bolívar: Distrito Piar, Macizo del Chimantá-tepui, cabeceras del afluente derecho superior del río Tirica ("Caño del Grillo"), ca. 2,450 m alt., Lat. 5°18′N, Long. 62°03′W, 7–8 Feb. 1983, *Julian A. Steyermark, Otto Huber & Victor Carreño E. 128945* (holotype, US; isotype, VEN).

Planta e fragmentis perveteribus solum cognita, florigera plus quam 46 cm alta. Folia superiora 13 cm longa; vaginis brevibus amplis; laminis anguste triangularibus, ad 12 mm latis, integris, utrinque minutissime obscureque lepidotis.

Scapus rectus, 5 mm diametro; scapi bracteis erectis, verisimiliter internodia superantibus. Inflorescentia laxe bipinnatim paniculata; bracteis primariis ignotis sed sine dubio ramorum basibus sterilibus brevissimis longioribus; ramis rectis, divergentibus, 8 cm longis, subdense florigeris. Bracteae florigerae angustissime triangulares, sepala subaequantes, floribus sessilibus. Sepala late ovata, ca. 5 mm longa. Capsula ovoidea; seminibus bicaudatis.

Leaf anatomy. Vascular bundles not recessed in or covered by chlorenchyma adaxially, broadly covered by chlorenchyma abaxially; adaxial water storage cells multi-stratose, the outermost layer resiniferous; adaxial subepidermal cells uni-stratose, vertically elongate, incrassate, abaxial subepidermal cells tri-stratose, isodiametric, strongly incrassate; substomatal pores constricted between the oblong, resiniferous lateral subsidiary cells.

The species can be distinguished in *Lindmania* by the very thick subepidermal layering on the abaxial surface of the leaf and the constriction of the substomatal pore between the prominent lateral subsidiary cells. The massive abaxial chlorenchyma is like that previously noted in *L. subsimplex* which is possibly closely related.

Known only from the type.

3. **Lindmania gracillima** (L. B. Smith) L. B. Smith, comb. nov. *Cottendorfia gracillima* L. B. Smith, Phytologia 7: 418, pl. 1, figs. 3–5. 1961.

4. *Lindmania wurdackii* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 284, fig. 13. 1957. *Cottendorfia wurdackii* (L. B. Smith) L. B. Smith, Phytologia 7: 171. 1960.

4.1. **Lindmania lateralis** (L. B. Smith & R. W. Read) L. B. Smith & H. Robinson, comb.

FIGURES 1–4.—1. *Lindmania sessilis,* Smith, Steyermark & Robinson.—2. *Lindmania saxicola* Smith, Steyermark & Robinson.—3. *Lindmania aurea* Smith, Steyermark & Robinson.—4. *Lindmania imitans* Smith, Steyermark & Robinson.

nov. *Cottendorfia lateralis* L. B. Smith & R. W. Read, Phytologia 30: 289, pl. 1. 1975.

The species description is emended by the following observations of leaf anatomy: Vascular bundles not covered with chlorenchyma adaxially or abaxially; adaxially water storage cells mostly 2–3-stratose, abaxially in distinct narrow canals; subepidermal cells adaxially 1–2-stratose, often resiniferous, not or scarcely incrassate; substomatal pores not occluded, oval or rounded; abaxial scales rudimentary, rarely with a few projecting cells.

The leaf cross-section is of the most typical *Lindmania* type as seen in *L. guianensis* and *L. argentea.*

5. *Lindmania paludosa* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 284, fig. 14. 1957. *Cottendorfia paludosa* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.
6. *Lindmania cylindrostachya* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 286, fig. 15. 1957. *Cottendorfia cylindrostachya* (L. B. Smith) L. B. Smith, Phytologia 7: 169. 1960.
7. **Lindmania savannensis** (L. B. Smith) L. B. Smith, comb. nov. *Cottendorfia savannensis* L. B. Smith, Mem. N.Y. Bot. Gard. 10(2): 16, fig. 3. 1960.

7.1. **Lindmania atrorosea** (L. B. Smith, Steyermark & Robinson) L. B. Smith, comb. nov. *Cottendorfia atrorosea* L. B. Smith, Steyermark & Robinson in Steyermark et al., Brittonia 33: 28, figs. 1, 2E, F. 1981.

8. **Lindmania nubigena** (L. B. Smith) L. B. Smith, comb. nov. *Cottendorfia nubigena* L. B. Smith, Mem. N.Y. Bot. Gard. 10(2): 16, fig. 2. 1960.
9. **Lindmania dyckioides** (L. B. Smith) L. B. Smith, comb. nov. *Cottendorfia dyckioides* L. B. Smith, Mem. N.Y. Bot. Gard. 14(3): 21, fig. 1. 1967.
10. *Lindmania argentea* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 414, fig. 78. 1957. *Cottendorfia argentea* (L. B. Smith) L. B. Smith, Phytologia 7: 169. 1960.
11. *Lindmania phelpsiae* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 286, fig. 16. 1957. *Cottendorfia phelpsiae* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.
12. **Lindmania dendritica** (L. B. Smith) L. B. Smith, comb. nov. *Cottendorfia dendritica* L. B. Smith, Mem. N.Y. Bot. Gard. 18(2): 31, fig. 5c. 1969.
13. **Lindmania longipes** (L. B. Smith) L. B. Smith, comb. nov. *Cottendorfia longipes* L. B. Smith, Mem. N.Y. Bot. Gard. 14(3): 22, fig. 2. 1967.
14. *Lindmania geniculata* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 414, fig. 79. 1957. *Cottendorfia geniculata* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.

14b. **Lindmania geniculata** var. **minor** (L. B. Smith, Steyermark & Robinson) L. B. Smith, comb. nov. *Cottendorfia geniculata* var. *minor* L. B. Smith, Steyermark & Robinson in Steyermark et al., Acta Bot. Venez. 14(3): 15. 1984.

15. *Lindmania guianensis* (Beer) Mez, DC. Monogr. Phan. 9: 537. 1896. *Anoplophytum guianense* Beer, Bromel 44. 1857. *Cottendorfia guianensis* (Beer) Baker, Handb. Bromel. 129. 1889.

15b. **Lindmania guianensis** var. **vestita** (L. B. Smith) L. B. Smith, comb. nov. *Cottendorfia guianensis* var. *vestita* L. B. Smith, Phytologia 7: 419. 1961.

16. **Lindmania maguirei** (L. B. Smith) L. B. Smith, comb. nov. *Cottendorfia maguirei* L. B. Smith, Mem. N.Y. Bot. Gard. 18(2): 31, fig. 5d, e. 1969.
17. *Lindmania brachyphylla* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 416, fig. 80. 1957. *Cottendorfia brachyphylla* (L. B. Smith) L. B. Smith, Phytologia 7: 169. 1960.

17b. **Lindmania brachyphylla** var. **angustior** (L. B. Smith, Steyermark & Robinson) R. W. Read, comb. nov. *Cottendorfia brachyphylla* var. *angustior* L. B. Smith, Steyermark & Robinson in Steyermark et al., Brittonia 33(1): 28. 1981.

18. *Lindmania steyermarkii* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 416, fig. 81. 1957. *Cottendorfia steyermarkii* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.
19. *Lindmania tillandsioides* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 416, fig. 82. 1957. *Cottendorfia tillandsioides* (L. B. Smith) L. B. Smith, Phytologia 9: 171. 1960.

19.1. **Lindmania riparia** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 5, 27q–t. TYPE: Venezuela. Bolívar: Auyan-tepui, along margins of stream, cumbre de la parte sur, meseta de piedra arenisca, entre "Oso Woods Camp" y "Libertador", 2,050–2,300 m alt., 15 May 1964, *Julian A. Steyermark 93895* (holotype, US; isotypes, MAC, NY).

FIGURES 5–8.—5. *Lindmania riparia* Smith, Steyermark & Robinson.—6. *Lindmania piresii* Smith, Steyermark & Robinson.—7. *Lindmania terramarae* Smith, Steyermark & Robinson.—8. *Lindmania huberi* Smith, Steyermark & Robinson.

Caulescens, florigera 2 dm alta, caule (apice) 1 cm diametro. Folia superiora 4 dm longa; vaginis vix distinctis; laminis lineari-lanceolatis, 35 mm latis, subtus minutissime lepidotis, angustissime albido-marginatis, basi minutissime denticulatis.

Scapus brevis, crassus; scapi bracteis foliaceis, erectis, dense imbricatis. Inflorescentia dense bipinnatim paniculata, 15 cm longa, trichomatibus subulatis fragilibus basi hemisphaericis persistentibus laxe vestita; bracteis primariis subfoliaceis, ramorum bases steriles superantibus. Bracteae florigerae lanceolatae, pedicellos crassos superantes; sepalis ellipticis, 5 mm longis, late albido-marginatis; petalis unguiculatis, albis (Steyermark).

Leaf anatomy. Vascular bundles adaxially deeply recessed in but not covered by chlorenchyma, abaxially narrowly covered by chlorenchyma; water storage cells adaxially 3–4-stratose, abaxially ca. 3-stratose in distinct canals; subepidermal cells in single subdistinct layers with slightly thickened walls; substomatal pores not occluded, oval to rounded with slightly thickened walls; abaxially with scales minute, irregularly peltate or shortly strap-shaped, with cells transversely oblong.

The leaf cross-section is like that seen in *Lindmania* in *L. tillandsioides, L. brachyphylla,* and the newly described *L. sessilis.* Both the key and the anatomy indicate closest relationship to *L. tillandsioides.* In spite of the close proximity in the key, *L. stenophylla* lacks the chlorenchyma abaxial to the vascular bundles, and it is probably not closely related.

Known only from the type.

20. *Lindmania subsimplex* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 417, fig. 83. 1957. *Cottendorfia subsimplex* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.

20.1. **Lindmania arachnoidea** (L. B. Smith, Steyermark & Robinson) L. B. Smith, comb. nov. *Cottendorfia arachnoidea* L. B. Smith, Steyermark & Robinson in Steyermark et al., Acta Bot. Venez. 14(3): 9, figs. 7, 10l–n. 1984.

20.2. **Lindmania aurea** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 3, 27i–m. TYPE: Venezuela. Bolívar: Distrito Piar, Macizo del Chimantá, pequeñas altiplanicies en la base septentrional de las farallones superiores del Amuri-tepui (Sector Oeste del Acopán-tepui), por escarpado encima de una cascada al oeste del acampamento, ca. 1,850 m alt., Lat. 5°10′N, Long. 62°07′ Oeste, 2–5 Feb. 1982, *Julian A. Steyermark, Otto Huber & Victor Carreño E. 128611* (holotype, US; isotypes, NY, VEN).

Breviter caulescens, florigera ca. 20 cm alta, leviter curvata, ascendens. Folia densissime rosulata, ad 12 cm longa, squamis minutissimis orbicularibus dense sed obscure vestita; vaginis brevibus, latis; laminis angustissime triangularibus, longe attenuatis, 5 mm latis, integris.

Scapus gracillimus, glaber; scapi bracteis erectis, subfoliaceis, angustissimis quam internodis longioribus sed scapum haud occultantibus. Inflorescentia simplex, sublaxa, 7 cm longa, glabra. Bracteae florigerae eis scapi simulantes, pedicellos inferiores superantes; pedicellis divergentibus, gracilibus, ad 9 mm longis. Sepala ovata, obtusa, 3 mm longa, tenuia; petalis spathulatis, 10 mm longis, aureis (Steyermark); ovario supero; ovulis caudatis.

Leaf anatomy. Vascular bundles not covered by chlorenchyma adaxially, narrowly covered abaxially; adaxial water storage cells mostly 2–3-stratose, abaxially cells smaller and bistratose in distinct but nearly contiguous canals; subepidermal cells unistratose adaxially and abaxially, with walls thickened in exterior half; substomatal pores not occluded, oval or rounded; abaxially scales rudimentary, eccentrically peltate, sometimes strap-shaped, cells transversely oblong.

Leaf anatomy is notable for the rounded, nonrecessed vascular bundles with a narrow abaxial covering of chlorenchyma and for the nearly continuous layer of abaxial water storage tissue. As such, the species does not seem closely related to most of the species with simple inflorescences with which it falls in the key. Closest relationship may be to *L. imitans* described below.

Known only from the type.

20.3. **Lindmania imitans** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 4, 27n–p. TYPE: Venezuela. Bolívar: Distrito Piar, Macizo del Chimantá, pequeñas altiplanicies en la base septentrional de los farallones superiores del Amurí-tepui (Sector W del Acopán-tepui), on vertical small bluff east of camp, Lat. 5°10′N, Long. 62°07′W, ca. 1,850 m alt., 2–5 February 1983, *Julian A. Steyermark, Otto Huber & Victor Carreño E. 128474* (holotype, US; isotype, VEN).

Breviter caulescens, florigera ca. 9 cm alta, leviter curvata, ascendens. Folia densissime rosulata, ad 12 cm longa, squamis minutissimis orbicularibus dense sed obscure vestita; vaginis brevibus, latis; laminis anguste triangularibus, attenuatis, 10 mm latis, integris.

Scapus gracillimus, glaber; scapi bracteis erectis, dense

imbricatis, subfoliaceis. Inflorescentia simplex, laxa, 5 cm longa, glabra. Bracteae florigerae eis scapi simulantes, pedicellos inferiores subaequantes; pedicellis divergentibus, gracilibus, ad 7 mm longis. Sepala suborbicularia, 3.5 mm longa; ovario supero.

Leaf anatomy. Vascular bundles not covered with chlorenchyma adaxially or abaxially, often with fiber-sheath extending to the epidermis; adaxial water storage cells 3–5-stratose; subepidermal cells smaller, unistratose, slightly incrassate; substomatal pores not occluded, oval or rounded; points of attachment of abaxial scales not seen, evidently very sparse.

The species has some resemblance to *L. aurea* with which it falls in the key, and it may be comparatively closely related. Nevertheless, the leaf cross-sections are strikingly different. The vascular bundles of the present species tend to be connected by fibers to the abaxial epidermis while the equivalent area in *L. aurea* is occupied by well developed water storage canals.

Known only from the type.

21. *Lindmania thyrsoidea* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 287, fig. 17. 1957. *Cottendorfia thyrsoidea* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.

21.1. **Lindmania smithiana** (Steyermark & Luteyn) L. B. Smith, comb. nov. For leaf anatomy see note under *Connellia varadarajanii*. *Connellia smithiana* Steyermark & Luteyn, Journ. Brom. Soc. 35: 152, fig. 3. 1985. Error in *C. varadarajanii* 35: fig. 1 on p. 52. 1985.

22. *Lindmania stenophylla* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 417, fig. 84. 1957. *Cottendorfia stenophylla* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.

23. *Lindmania minor* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 419, fig. 85. 1957. *Cottendorfia minor* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.

23.1. **Lindmania piresii** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 6, 27u–x. TYPE: Brazil. Amazonas: Serra Araca, 10 February 1975, *J. M. Pires 15.010(33)* (holotype, US; isotype, IPEAN).

Caulescens, florifera 1–1.5 m alta (Pires); caule 30–50 cm alto. Folia ultra 4 dm longa; vaginis ellipticis, 4 cm longis; laminis anguste triangularibus, perattenuatis, 18 mm latis, subtus trichomatibus fimbriatis albis vestitis, glabrescentibus, basi laxe serrulatis.

Scapus rectus, gracilis, glabrescens; scapi bracteis ex basi brevi ovata longe angustissimeque laminatis, internodia superantibus. Inflorescentia laxe bipinnatim paniculata, glabrescens sed trichomatum basibus glanduliformibus persistentibus; bracteis primariis eis scapi similibus, ramorum bases subaequantibus; ramis patentibus, ad 12 cm longis, laxe florigeris. Bracteae florigerae triangulares, 2 mm longae; pedicellis patentibus, 4–5 mm longis. Sepala late ovata, obtusa, 3 mm longa, basi sulcata, apice scariosa; petalis 7 mm longis, albis.

Leaf anatomy. Vascular bundles not covered adaxially or abaxially by chlorenchyma; water storage cells forming distinct abaxial canals; subepidermal cells adaxially and abaxially 1–2-stratose, often resiniferous, not or scarcely incrassate; substomatal pores not occluded, oval or rounded; abaxial scales peltate, with a fringe of elongate, contorted cells.

The leaf cross-section is of the most typical *Lindmania* type as seen in *L. guianensis, L. argentea,* and relationship is probably to that group. Most of the related species can be distinguished by either having primary bracts in the inflorescence shorter than the sterile bases of the branches or having floral bracts equalling or exceeding the length of the pedicels.

Known only from the type.

23.2. **Lindmania terramarae** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 7, 29a–d. TYPE: Venezuela. Amazonas: Dept. Atabapo, Cerro Marahuaca, cumbre, extremo sureste, alrededor de una lagunita, altura 2,800 metros, Lat. 3°35′N, Long. 65°20′ Oeste, 26 March 1983, *Julian A. Steyermark & Francisco Delascio 129067* (holotype, US; isotypes, NY, VEN).

Acaulis (Steyermark), e fragmentis solum cognita sed verisimiliter 2 m alta. Folia ca. 4 dm longa; vaginis brevibus amplis; laminis anguste triangularibus, ad 3 cm latis, base laxe spinoso-serrulatis, subtus lepidotis.

Scapus rectus, robustus, glaber; scapi bracteis erectis, inferioribus ignotis sed verisimiliter subfoliaceis dense imbricatisque, superioribus internodia paulo superantibus sed angustissimis et scapum haud occultantibus. Inflorescentia verisimiliter cylindrica, laxe bipinnatim paniculata, glabra; bracteis primariis angustissimis, quam ramorum basibus sterilibus longioribus; ramis suberectis vel divergentibus, ad 12 cm longis, sublaxe florigeris. Bracteae florigerae late ovatae attenuatae, 4 mm longae; pedicellis patentibus, gracilibus, 6 mm longis. Sepala late ovata, acuta, 5 mm longa, tenuia; petalis 12 mm longis. Capsula ovoidea.

Leaf anatomy. Vascular bundles recessed in chlorenchyma and reached by narrow extensions of water storage tissue adaxially and abaxially,

only smaller bundles sometimes covered abaxially; water storage cells adaxially and abaxially 2–3-stratose with tenuous walls, abaxially forming broad often contiguous canals; subepidermal cells 2–3-stratose adaxially and abaxially, firm and often resiniferous, walls thickened in only the exterior parts of the outermost cells; substomatal pores not occluded, oval; abaxially with numerous rudimentary scales that do not bear a distinct disc.

Lindmania terramarae shows the type of leaf anatomy common in the large typical group of *Lindmania*. It is probably most closely related to *L. marahuacae*, from the same mountain, with which it shares a comparatively glabrous condition. The new species differs by the taller, straighter inflorescence and the more verrucose leaves. Anatomically the leaves seem to have more highly developed layers of subepidermis, that layer being scarcely distinct in *L. marahuacae*.

23.3. **Lindmania marahuacae** (L. B. Smith, Steyermark & Robinson) L. B. Smith, comb. nov. *Cottendorfia marahuacae* L. B. Smith, Steyermark & Robinson in Steyermark et al., Acta Bot. Venez. 14, no. 3: 9, fig. 1, k–r. 1984.

24. *Lindmania navioides* L. B. Smith, Mem. N.Y. Bot. Gard. 9: 419, fig. 86. 1957. *Cottendorfia navioides* (L. B. Smith) L. B. Smith, Phytologia 7: 170. 1960.

24.1. **Lindmania huberi** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 8, 28a–d. TYPE: Venezuela. Bolívar: Distrito Pilar, Macizo del Chimantá, pequenas altiplanicies en la base septentrional de los farallones superiores del Amurí-tepui (Sector Oeste del Acopan-tepui) en la base de cañon pequeno debajo del campamento donde el agua corre, ca. 1,850 m alt., Lat. ca. 5°10′N, Long. 62°07′ Oeste, 2–5 February 1983, *Julian A. Steyermark, Otto Huber & Victor Carreño E. 128465* (holotype, US; isotypes, NY, VEN). PARATYPE: Venezuela. Bolívar: Cumbre del Macizo de Chimantá, Sector nor-oriental, Tirepón (Torono)-tepui, Lat. 5°22′N, Long. 61°58′ Oeste, 2,540 m alt., 24 February 1978, *Julian A. Steyermark, Victor Carreño E., Roy McDiarmid & Charles Brewer-Carias 115846* (US, VEN).

Caulescens, florigera 13 cm alta, caule robustissimo ad 10 cm longo. Folia multa, in apicibus ramorum dense rosulata, 9 cm longa; vaginis brevibus, omnino occultantibus; laminis anguste triangularibus, curvatis, eis inferioribus recurvatis, 10 mm latis, pungentibus, integris, glabris, glaucis (Steyermark), vix cretaceis.

Inflorescentia sessilis, corymbiformis, multiflora. Bracteae florigerae angustissime triangulares; pedicellis elongatis, gracilibus. Sepala suborbicularia, 3.5 mm longa, libera, inflata, nervata, squamis minutissimis dense vestita; petalis spathulatis, 6 mm longis, cremeis (Steyermark); antheris suborbicularibus, equitantibus; ovario supero; ovulis caudatis.

Leaf anatomy. Vascular bundles not covered by chlorenchyma adaxially or abaxially, not recessed in chlorenchyma adaxially, with fiber sheath extending to the epidermis abaxially; water storage cells inflated, ca. 4-stratose; subepidermal cells on both surfaces in one layer, with walls slightly incrassate; substomatal pores not occluded, rounded; pits bearing abaxial scales not seen, evidently very sparse.

Abaxially buttressed vascular bundles have been previously noted in *Lindmania* in *L. navioides, L. minor, L. thyrsoidea,* and the newly described *L. imitans,* all of which fall in separate places in the key, and none of which seem particularly closely related. Because of the sessile inflorescence, the new species keys out with *L. navioides,* but the latter represents a totally distinct element in the genus with elongate flexuous stems and densely imbricate, spreading, thin-textured leaves. The thicker leaves of *L. huberi* with the non-contoured upper epidermis indicate relationship to the more typical element of *Lindmania.*

Known only from the type and paratype.

5.1. **STEYERBROMELIA** L. B. Smith in Steyermark et al., Acta Bot. Venez. 14(3): 8. 1984. TYPE: *Steyerbromelia discolor* L. B. Smith & Robinson in Steyermark et al., sp. nov. Acta Bot. Venez. 14(8): 8. 1984.

Plants rosulate; leaves spinose-serrate, anatomy similar to *Lindmania* except substomatal pores usually partially occluded; inflorescence compound; flowers sessile, not or scarcely narrowed below; sepals imbricate; petals regular, appendaged with two vertically attached scales; stamens equal; ovary wholly superior, style branches often broadly lamelliform or lobed; seeds bicaudate.

The genus is known only from central Amazonas in Venezuela. Closest relationship is evidently to *Lindmania* from which it differs by the imbricated sepals and the appendaged petals.

Nomenclatural note: *Steyerbromelia* was originally prepared as a monotypic genus with *S. discolor* as the only species. *Steyerbromelia deflexa* was then added to the manuscript, but the resulting need to indicate a type species was overlooked. Cf. International Code Articles 37, 43.

1a. Branches suberect. Marahuaca ..... 1. *S. discolor*
1b. Branches decurved.
  2a. Leaf-blades glabrous. Duida ..... 2. *S. deflexa*
  2b. Leaf-blades densely cinereous-lepidote beneath. Aratitiyope ..... 3. *S. diffusa*

1. *Steyerbromelia discolor* L. B. Smith & Robinson in Steyermark et al., Acta Bot. Venez. 14(3): 8, figs. 2a–i, 6i–k. 1984.
2. *Steyerbromelia deflexa* L. B. Smith & Robinson in Steyermark et al., Acta Bot. Venez. 14(3): 12, figs. 3a–f, 10i–k. 1984.

3. **Steyerbromelia diffusa** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 9, 28e–i. TYPE: Venezuela. Amazonas: Dept. Río Negro, Cerro Aratitiyope, piedra ignea, 990–1,670 m alt., Lat. 2°10′N, Long. 65°34′ Oeste, ca. 70 km SSO de Ocamo, con riachuelos afluente al rio Manipitare, 24 Feb. 1984, *Julian A. Steyermark, Paul Berry & Francisco Delascio 130072* (holotype, US; isotypes, NY, VEN).

Verisimiliter caulescens, florifera ultra 3 m alta. Folia ca. 1 m longa, rosulata, vetera patentia, juvenalia ascendentia, vaginis brevibus, amplis; laminis angustissime triangularibus, ca. 35 mm latis, supra lucidis, atro-viridibus (! Steyermark), mox glabris, subtus dense adpresseque cinereo-lepidotis, laxe spinoso-serrulatis.

Scapus cylindricus, glaber; scapi bracteis erectis, infirmis, subfoliaceis, internodia multo superantibus, supremis late ovatis, attenuatis. Inflorescentia laxissime 3-pinnatim paniculata; bracteis primariis late ovatis, acuminatis, quam ramorum basibus sterilibus elongatis multo brevioribus, ramis per anthesin divergentibus, ultra 6 dm longis, ramulis gracillimis, senectis decurvatis. Bracteae florigerae reflexae, suborbiculares, 2 mm longae, apiculatae; floribus subsessilibus, patentibus. Sepala ovata, acuta, 5 mm longa, duabus inferioribus nervo mediano crasso auctis; petalis 7 mm longis, albis (Steyermark); ovario supero; ovulis caudatis.

Leaf anatomy. Vascular bundles not covered by chlorenchyma adaxially or abaxially, abaxially with fiber sheath extending to epidermis; adaxial water storage cells mostly 3–5-stratose, outermost and innermost mostly resiniferous; adaxial and abaxial subepidermal cells small, walls incrassate in part nearest epidermis, abaxial cells sporadically resiniferous; substomatal cells with unthickened walls, bearing pairs of papillae protruding into pore; abaxially with subrotund scales, with smaller cells toward the dentate and denticulate margin.

Available material of flowers shows that the present species differs from the other two by the more elongate bases of its petals and its less broadened style branches. This third species of *Steyerbromelia* shows yet a third variation in the leaf cross-section with the vascular bundles extending abaxially to the epidermis. In *S. deflexa* the area abaxial to the bundles has a layer of chlorenchyma and one to three layers of small hyaline cells. In *S. discolor* the same area has well developed water storage canals. Nevertheless, evidence seems to show that the genus may be phyletically sound in spite of such differences. The new species and *S. discolor* have essentially identical structure of their abaxial leaf scales. Also, both have intrusions into their substomatal pores that is unlike any *Lindmania*. The third species, *S. deflexa,* has only rudimentary abaxial scales that cannot be compared while its substomatal pores tend to be somewhat irregular with some short intrusions.

Known only from the type.

8. **PITCAIRNIA** L'Héritier, Sert. Angl. 7. 1788; nom. conserv.

REVISED SEGMENTS OF KEY TO SUBGENUS *PEPINIA*

9. Inflorescence bipinnate; sepals acute.
  9a. Primary bracts of inflorescence narrowly triangular, acuminate, 10 cm long; pedicels stout, costate, ca. 10 mm long; floral bracts 10 mm long; sepals 35 mm long. Colombia, Venezuela ..... 6. *P. bulbosa*
  9a. Primary bracts broadly ovate, to 6 cm long; pedicels slender, to 18 mm long; floral bracts 5 mm long; sepals 16 mm long. Brazil; Amazonas ..... 6.1. *P. rondonicola*
9. Inflorescence tripinnate; sepals obtuse, 20 mm long. Colombia ..... 7. *P. heliophila*

30a. Scapes short, recurved; inflorescence densely flowered, secund; sepals filiform-attenuate. Yutaje ..... 19.2. *P. nematophora*
30a. Scapes erect; inflorescence lax, not secund; sepals acute.
  30b. Leaves densely furfuraceous beneath; petals ca. 50 mm long and 7 mm wide. Amazonas of Brazil and Venezuela ..... 19. *P. platypetala*
  30b. Leaves essentially glabrous on both surfaces; petals narrower. Tumaque-Humaque, Brazil ..... 19.1. *P. sastrei*

FIGURES 9–12.—9. *Steyerbromelia diffusa* Smith, Steyermark & Robinson.—10. *Navia plowmanii* Smith, Steyermark & Robinson.—11. *Navia thomasii* Smith, Steyermark & Robinson.—12. *Navia polyglomerata* Smith, Steyermark & Robinson.

6.1. *Pitcairnia rondonicola* L. B. Smith & R. W. Read, J. Brom. Soc. 36(1): 10, fig. 4. 1986.

19. *Pitcairnia platypetala* Mez in Mart., Fl. Bras. 3(3): 438. 1894, emend. L. B. Smith & Read, Brittonia 33: 33. 1981.

19.2. *Pitcairnia nematophora* L. B. Smith & Read, Brittonia 33: 31. 1981.

9. **BROCCHINIA** Schult. f. in Roem. & Schult. Syst. 7(2): lxx, 1250. 1830.

1a. Leaves and scape-bracts serrate; ovary only one-third inferior. Colombia, Venezuela ..... 1. *B. serrata*
1b. Leaves and bracts always entire; ovary wholly or almost wholly inferior.
2a. Leaves even above, 14–30 cm long. Venezuela, Amazonas.
3a. Inflorescence glabrous or subglabrous, petals unguiculate. Cerro Sipapo (Paraque) ..... 2. *B. maguirei*
3b. Inflorescence lepidote; petals elliptic or oblong-elliptic.
4a. Leaf-blades narrowly triangular; upper scape-bracts shorter than the internodes; sepals cucullate; inflorescence tripinnate. Duida ..... 3. *B. vestita*
4b. Leaf-blades ligulate; scape-bracts all much exceeding the internodes.
5a. Inflorescence tripinnate; sepals and petals obtuse. Cerro Parú, Río Ventuari ..... 4. *B. hitchcockii*
5b. Inflorescence bipinnate; sepals and petals acute. Cerro Moriche, Río Ventuari ..... 5. *B. cowanii*
2b. Leaves prominently nerved on both sides, 16–120 cm long.
6a. Blades ligulate, rounded and apiculate.
7a. Inflorescence glabrous; stem columnar; plant to 8 m high. Eastern Bolívar and adjacent Guyana ..... 11. *B. micrantha*
7b. Inflorescence lepidote.
8a. Branches strict, the lowest with the basal flowers covered by the large primary bracts; inflorescence very narrow. Amazonas: Cerro Yapacana ..... 13. *B. cryptantha*
8b. Branches divergent to spreading, much exceeding the primary bracts; inflorescence broad.
9a. Central and secondary axes straight; leaves divergent to spreading.
10a. Leaf-blades very narrowly castaneous-margined; sepals oblong; petals unguiculate; styles free, thick. Southeastern Colombia and adjacent Venezuela ..... 14. *B. paniculata*
10b. Leaf-blades concolorous; sepals and petals subequal, elliptic; styles basally connate, slender; plant highly variable. Bolívar and Amazonas ..... 15. *B. tatei*
9b. Central and secondary axes flexuous or geniculate; leaves erect or suberect.
11a. Leaves forming a tight tube; scape about 3 mm in diameter, its upper bracts 1–2 cm long, remote; inflorescence rarely more than bipinnate. Bolívar and adjacent Guyana ..... 17. *B. reducta*
11b. Leaves suberect, separate for most of their length; scape much stouter with large bracts; inflorescence distinctly tripinnate. Southeastern Colombia to eastern Venezuela ..... 18. *B. hechtioides*
6b. Blades acute or acuminate.
12a. Blades subpetiolate, linear-lanceolate, 3 cm wide; inflorescence tripinnate; primary bracts shorter than the sterile bases of the branches. Bolívar: Uriman ..... 6. *B. bernardii*
12b. Blades not constricted at base; inflorescence bipinnate to quadripinnate; primary bracts shorter than to slightly longer than the sterile bases of the branches.
13a. Blades with hard, thickened, pungent apices.
14a. Inflorescence densely lepidote; ovary sessile; blades subligulate. Neblina, Gran Sabana, Guyana ..... 12. *B. steyermarkii*
14b. Inflorescence glabrous or subglabrous; ovary pedicellate; blades narrowly triangular.
15a. Leaf-sheaths and apices dark castaneous. Southern Venezuela ..... 10. *B. melanacra*
15b. Leaf-sheaths and apices green.
16a. Capsules sharply 3-angled; inflorescence bipinnate, the ultimate branches elongate and laxly flowered. Gran Savanna, Cerro Yapacana ..... 9. *B. prismatica*
16b. Capsules terete; inflorescence amply tripinnate, the ultimate branches short and densely flowered. Southeastern Colombia and southern Venezuela ..... 8. *B. acuminata*
13b. Blades of the same texture throughout, ligulate or subligulate.
17a. Flowers secund; plant ca. 1.5 m high. Bolívar: Ptari-tepui ..... 16. *B. secunda*
17b. Flowers polystichous; plant ca. 0.5 m high.

18a. Blades linear, 4 mm wide; inflorescence bipinnate. Neblina ..... 7. *B. delicatula*
18b. Blades ligulate, 20 mm wide; inflorescence tripinnate. Brazil: Amazonas: Rio da Serra Aracá ..... 7.1. *B. amazonica*

7.1. *Brocchinia amazonica* L. B. Smith, Jour. Brom. Soc. 34: 106, fig. 4. 1984.

11. **NAVIA** Schult. f. in Roem. & Schult. Syst. 7(2): lxv, 1195. 1830.

KEY TO SUBKEYS OF *NAVIA*

1a. Inflorescence laxly racemose or paniculate ..... Subkey I
1b. Inflorescence glomerate or moniliform-glomerate.
2a. Ovary superior.
3a. Sepals free.
4a. Sepals acute or acuminate or attenuate, sometimes incurved but never cucullate ... Subkey II
4b. Sepals obtuse or subacute, often cucullate ..... Subkey III
3b. Sepals connate posteriorly or equally ..... Subkey IV
2b. Ovary partly or almost wholly inferior ..... Subkey V

Revised section of Subkey I

5. Spikes not strobilate, laxer.
7. Sepals 2–5 mm long, not alate.
8. Sepals ecarinate; plant little if any over 1 m high. Colombia ..... 6. *N. garcia-barrigae*
8. Posterior sepals carinate, plants 0.8–5 m high. Venezuela.
8a. Inflorescence bipinnate; plant 0.8 m high. Neblina ..... 6.1. *N. plowmanii*
8a. Inflorescence amply 3–4-pinnate, plants 2–5 m high.
9. Spikes digitate in threes, to 26 cm long. Amazonas: Cerro Sipapo (Paraque) ..... 7. *N. brocchinioides*
9. Spikes pinnate. Neblina.
9a. Central floral axis stout; leaves to 4 dm long; blades 27 mm wide; inflorescence glabrous ..... 8. *N. diffusa*
9a. Central floral axis slender; leaves 6 dm long; blades 10 mm wide; inflorescence lepidote ..... 8.1. *N. thomasii*

6.1. **Navia plowmanii** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 10, 28j–o. TYPE: Venezuela. Amazonas: Dept. Rio Negro, open rocky meadow on N facing slope with large granite outcrops, forming a ridge meadow at base of a large peak, vicinity of Camp VI, on a ridge on Venezuelan-Brazilian border, 3.5 km W of Pico Zuloaga, 2,000 m alt., Lat. 0°53′N, Long. 65°56′W, 13–15 April 1984, *W. W. Thomas & T. Plowman 3030* (holotype, US; isotypes, NY, VEN).

Planta vetusta solum cognita, caulescens, florigera 8 dm alta. Folia ad 14 cm longa; vaginis inconspicuis; laminis anguste triangularibus, 16 mm latis, supra glabris, subtus per aetatem glabrescentibus, laxe serrulatis.

Scapus 1 cm diametro, per aetatem glaber; scapi bracteis erectis, subfoliaceis, internodia superantibus sed vix occultantibus. Inflorescentia laxe bipinnatim paniculata; bracteis primariis late ovatis, quam ramorum basibus sterilibus brevioribus; ramis ad 7 cm longis. Bracteae florigerae late ovatae, acutae, quam sepalis subduplo brevioribus; floribus patentibus, sessilibus. Sepala imbricata, ovata, 4 mm longa; petalis ignotis; ovario supero; seminibus bicaudatis.

Leaf anatomy. Vascular bundles not covered by chlorenchyma adaxially; adaxial water storage cells multi-stratose, highly inflated, smaller outermost layer and innermost layer resiniferous; subepidermal cells resiniferous, adaxial narrow and strongly incrassate, abaxial similar, larger, less incrassate; substomatal pores nearly occluded, transversely elongate, halteriform; abaxial scales minute, eccentric, with transversely oblong cells.

This species is placed in *Navia* because of its imbricate sepals, although its appendaged seeds might suggest inclusion in *Lindmania*. Persistence of the ovule appendages into the mature state has been noted before in at least one other species of *Navia, N. scirpiflora*. As in that previous case, the presence of occluded substomatal pores confirms the generic placement in *Navia*.

Known only from the type.

8.1. **Navia thomasii** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 11, 28p–s. TYPE: Venezuela. Amazonas: Dept. Río Negro, dry

forest and scrub vegetation on ESE facing slope above Río Marawinuma E of "Puerto Chimo" camp, dominant on open slope, ca. 600 m alt., Lat. 0°50′N, Long. 66°07′W, 26 April 1984, *W. W. Thomas 3245* (holotype, US; isotypes, NY, VEN).

Planta e fragmentis solum cognita, florigera verisimiliter ca. 2 m alta. Folia superiora ad 6 dm longa; vaginis inconspicuis; laminis angustissime triangularibus, 10 mm latis, supra glabris, subtus dense albidolepidotis, laxe serrulatis.

Scapus 8 mm diametro, glabrescens; scapi bracteis erectis, foliaceis. Inflorescentia laxissime 4-pinnatim paniculata, lepidota; bracteis primariis verisimiliter late ovatis et quam ramorum basibus sterilibus multo brevioribus, ramis ad 25 cm longis. Bracteae florigerae late ovatae, quam sepalis duplo brevioribus; floribus patentibus, sessilibus. Sepala ovata, acuta, libera, 4 mm longa, ea posteriora obtuse carinata; petalis 6 mm longis, albis (Thomas); ovario supero.

Leaf anatomy. Vascular bundles not covered by chlorenchyma adaxially or abaxially, abaxially with fiber sheath reaching the epidermis; water storage cells multi-stratose, sporadically resiniferous, interior cells more tenuous, innermost less resiniferous; subepidermal cells adaxially small, incrassate, abaxially 1–2-stratose, scarcely incrassate, resiniferous; substomatal pore nearly occluded, transversely elongate, halteriform; abaxially scales small, peltate, lobed, with indistinct cells.

AMENDED SECTIONS OF SUBKEY II

3. Omit lead to 13. *Navia lopezii,* which proves to be a member of the Xyridaceae.

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9. Sepals 12–18 mm long; floral bracts straight; leaf-blades serrulate.
   10. Sepals glabrous or glabrescent, acute, inflorescences as in 11.
      10a. Inflorescence 15 mm in diameter, green. Duida ..... 19. *N. steyermarkii*
      10a. Inflorescence 40–50 mm in diameter, pink to red. Guanay, Yutaje ..... 20. *N. phelpsiae*
   10. Sepals laxly filamentous-lepidote, broadly acute, narrowly alate-carinate; inflorescence red, 2 cm in diameter. Duida-Huachamacari ..... 20.1. *N. aliciae*

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16. Sepals 5–8 mm long.
   16a. Inflorescence compound, digitate-globose from several ellipsoid spikes, many-flowered.
      16b. Inflorescence sessile; floral bracts broadly ovate, acute, about equaling the sepals. Amazonas-adjacent Brazil ..... 25. *N. crispa*
      16b. Inflorescence scapose; floral bracts ovate, long-attenuate, exceeding sepals. Amazonas: Río Marawinuma ..... 25.1. *N. polyglomerata*
   16a. Inflorescence simple, hemispherical, sessile. Amazonas: Duida-Río Orinoco ..... 25.2. *N. huberiana*

Navia lopezii should be transferred from the Bromeliaceae and placed in the Xyridaceae. The distinctive epidermis and lack of trichomes in the species have previously been noted by Robinson (1969). The species and its variety are disposed as follows:

13. *Araratitiyopea lopezii* (L. B. Smith) Steyermark & Berry, Ann. Missouri Bot. Gard. 71: 297, fig. 1. 1984. *Navia lopezii* L. B. Smith, Bot. Mus. Leafl. Harvard 15: 40. 1951; 16: 195, pl. 28. 1954; Fl. Neotrop. no. 14(1): 465, fig. 163L, M. 1974.

13b. *Aratitiyopea lopezii* var. *colombiana* (L. B. Smith) Steyermark & Berry, Ann. Missouri Bot. Gard. 71(1): 299. 1984. *Navia lopezii* var. *colombiana* L. B. Smith, Bot. Mus. Leafl. Harvard 16: 195. 1954; Fl. Neotrop. no. 14(1): 465. 1974.

20.1. *Navia aliciae* L. B. Smith, Steyermark & Robinson in Steyermark et al., Acta Bot. Venez. 14 (3): 13, figs. 9a–f, 10a–e. 1984.

25.1. **Navia polyglomerata** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 12, 28t–z. TYPE: Venezuela. Amazonas: On banks of Río Marawinuma, 2–6 km east of Base Camp, 160 m alt., Lat. 0°50′N, Long. 66°08′W, 26 April 1984, *W. W. Thomas 3261* (holotype, US; isotypes, NY, VEN). PARATYPES: Venezuela. Amazonas: Common on open slopes at ca. 550 m alt., dry forest and scrub vegetation on ESE facing slope on Río Marawinuma, east of "Puerto Chimo" camp, Lat. 0°50′N, Long. 66°07′W, 26 April 1984, *W. W. Thomas 3257* (NY, US, VEN). Dept. Río Negro: on moss-covered bank, 5–10 km east of Cerro de Neblina Base Camp which is on Río Marawinuma, Puerto Chimo Camp, 150 m alt., Lat. 0°50′N, Long. 66°07′W, 9 Feb. 1984, *R. Liesner & Charles Brewer 15807* (MO, US). Puerto Chimo Camp and up north slope of canyon, 5 km east of La Neblina Base Camp by air, 150–1,800 m, Lat. 0°50′N, Long. 66°07′W,

FIGURES 13–16.—13. *Navia huberiana* Smith, Steyermark & Robinson.—14. *Navia pedemontana* Smith, Steyermark & Robinson.—15. *Navia crassicaulis* Smith, Steyermark & Robinson.—16. *Navia linearis* Smith, Steyermark & Robinson.

11 Feb. 1984, *R. Liesner & Charles Brewer 15875* (MO, US).

Caulescens; caule erecto, robusto (ad 1 m alto). Folia ad 3(–4) dm longa; vaginis parvis, inconspicuis; laminis angustissime triangularibus, 7(–15) mm latis, utrinque trichomatibus subulatis fragilibus basi semiglobosis persistentibus laxe vestitis, integris, margine recurvatis, siccis linea mediana pallida auctis.

Scapus erectus, gracilis, 4 cm longus, sulcatus, trichomatibus eis laminarum similibus vestitus; scapi bracteis foliaceis, longissimis. Inflorescentia e spicis 5–7 digitata; bracteis primariis eas superiores scapi simulantibus, inflorescentiam superantibus; spicis ellipsoideis, dense multifloris, 25 mm longis. Bracteae florigerae dense imbricatae, ovatae, longe attenuatae, sepala superantes. Sepala libera, posteriora anguste triangularia, acuta, carinata, 8 mm longa, glabra; petalis albis (Thomas). Capsula subglobosa, 3 mm longa; seminibus in loculis solitariis, exappendiculatis.

Leaf anatomy. Vascular bundles narrowly covered by chlorenchyma adaxially and abaxially, narrower abaxially; water storage cells adaxially 1–3-stratose toward the margins, in the middle multistratose, abaxially in distinct canals under the vascular bundles; adaxial and abaxial subepidermal cells mostly indistinct, not incrassate, multistratose and incrassate adaxially in the middle of the leaf; substomatal pores not occluded, oval; abaxial surface with rudimentary uniseriate hairs.

The species could be close to *N. crispa* and other non-scapose species on the basis of leaf anatomy. The more strongly scapose *N. caulescens* of Colombia also seems related in spite of its multiseriate trichomes.

Known only from the Neblina area.

25.2. **Navia huberiana** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 13, 29e–h. TYPE: Venezuela. Amazonas: Dept. Atabapo, terrestre sobre los taludes de un caño, frecuente, bancos arenosos de un caño a unos 12 km al W de Esmeralda, entre el Cerro Duida y el Río Orinoco, preparado de material vivo entregado al Dr. Steyermark en Caracas, ca. 125 m alt., Lat. 3°11′N, Long. 65°37′W, 7 March 1980, *O. Huber 5058* (holotype, US; isotype, VEN).

Caulescens; caule erecto, brevi. Folia ad 13 cm longa; vaginis parvis, inconspicuis; laminis angustissime triangularibus, 6 mm latis, utrinque trichomatibus subulatis fragilibus basi semiglobosis persistentibus laxe vestitis, serrulatis, planis vel margine incurvatis, siccis linea mediana pallida auctis.

Inflorescentia sessilis, simplex, semiglobosa; bracteis primariis foliaceis, inflorescentiam superantibus. Bracteae florigerae ovatae, attenuatae, sepala superantes, virides, albo-tomentosae. Sepala libera, ovata, acuta, 7 mm longa, castanea, albo-tomentosa; ovario supero.

Leaf anatomy. Vascular bundles broadly covered by chlorenchyma adaxially and abaxially; subepidermal cells adaxially distinct, abaxially indistinct; substomatal cells with wall not incrassate, with paired simple papillae projecting into pore from each side; abaxially with short, uniseriate bulbous-based hairs.

The leaf section and the uniseriate hairs would place the new species in the general relationship of *Navia crispa,* but *N. huberiana* differs in the broader abaxial chlorenchyma over the veins and the paired simple papillae projecting into the substomatal pores.

Known only from the type.

Revised Subkey III

1. Inflorescence or its branches digitate-compound.
   2. Inflorescence slenderly scapose. Bolívar: Jáua.
      3. Cluster of spikes single ..... 39.3. *N. luzuloides*
      3. Clusters of spikes many, widely spaced on a long axis ..... 39.4. *N. scirpiflora*
   2. Inflorescence sessile or subsessile.
      4. Inner leaf-blades white at anthesis; sepals 10 mm long, much exceeding the floral bracts. Bolívar: Jáua ..... 39.2. *N. jauana*
      4. Inner leaf-blades like those below.
         5. Sepals 13–14 mm long.
            6. Floral bracts ovate, attenuate; leaves 10 cm long, the blades 9 mm wide, involute. Bolívar: Jáua ..... 39. *N. robinsonii*
            6. Floral bracts broadly rounded and apiculate; leaves over 30 cm long, the blades 17 mm wide, flat. Amazonas: Río Cunucunuma ..... 39.1. *N. pedemontana*
         5. Sepals 7–7.5 mm long. Bolívar.
            7. Floral bracts broadly ovate, about equaling the sepals; leaves 30 cm long, the blades 9 mm wide. Ichún ..... 40. *N. navicularis*
            7. Floral bracts suborbicular, distinctly shorter than the sepals; leaves 3 cm long, the blades 20 mm wide. Jáua ..... 41. *N. breweri*

1. Inflorescence simple.
   8. Leaf-blades 8–20 mm wide.
      9. Keel of the posterior sepals dilated below the apex; inflorescence few-flowered. Amazonas: Duida ..... 35. *N. xyridiflora*
      9. Keel of the posterior sepals linear or broader at base or middle.
         10. Sides of the posterior sepals 1 mm wide, their keels very narrow.
            11. Leaf-blades densely cinereous-lepidote beneath, their sides contrasting.
               12. Leaves and bracts finely subulate-attenuate; posterior sepals incurved but not cucullate. Amazonas: Marahuaca ..... 36. *N. pauciflora*
               12. Leaves and bracts apically thickened and obtuse; sepals cucullate. Bolívar: Jáua ..... 37. *N. incrassata*
            11. Leaf-blades sparsely lepidote on both sides, becoming glabrous.
               13. Floral bracts oblong, broadly acute. Bolívar: Pauo, Río Caura ..... 38. *N. caurensis*
               13. Floral bracts broad, broadly rounded.
                  14. Floral bracts suborbicular, entire. Bolívar: Guaiquinima ..... 38.1. *N. ovoidea*
                  14. Floral bracts oblong, serrulate, cucullate. Amazonas: Duida ..... 38.2. *N. albiflora*
         10. Sides of the posterior sepals 2 mm wide, their keels narrow or broad.
            15. Leaf-blades cretaceous beneath. Amazonas.
               16. Floral bracts serrulate; sepals strongly nerved, lepidote: leaf-blades 20 mm wide. Duida ..... 44. *N. latifolia*
               16. Floral bracts entire; sepals even, glabrous; leaf-blades 13 mm wide. Huachamacari ..... 45. *N. cretacea*
            15. Leaf-blades sparsely and minutely lepidote on both sides, becoming glabrous.
               17. Inflorescence subglobose.
                  18. Floral bracts pandurate, broadly rounded and apiculate, serrulate, lepidote; blades glabrous. Amazonas: Duida ..... 42. *N. octopoides*
                  18. Floral bracts acute, the inner ones entire, glabrous; leaf-blades white-barbellate in the axils of the spines. Guyana ..... 43. *N. barbellata*
               17. Inflorescence narrow, largely covered by the subfoliaceous bracts. Amazonas.
                  19. Leaf-blades narrowly triangular, 18 mm wide; caudex stout, 30 cm tall. Neblina ..... 43.1. *N. crassicaulis*
                  19. Leaf-blades linear, contracted toward base, 9 mm wide; caudex short. Marahuaca ..... 43.2. *N. linearis*

8. Leaf-blades not over 6 mm wide.
   20. Leaf-blades entire or serrulate only near base, 6–20 cm long, most species over 12 cm long.
      21. Floral bracts obtuse.
         22. Leaf-blades covered beneath with appressed cinereous scales; leaf blades 5 mm wide. Amazonas: Yutaje ..... 51. *N. umbratilis*
         22. Leaf-blades glabrescent except for the densely white-ciliate margins.
            23. Leaves numerous; blades mostly 3 mm, rarely to 5 mm wide; inflorescence many-flowered, ovoid. Amazonas: Cerro Vinilla ..... 51.1. *N. culcitaria*
            23. Leaves relatively few; blades uniformly 5 mm wide; inflorescence few-flowered, fasciculate. Brazil: Amazonas ..... 51.2. *N. piresii*
      21. Floral bracts acute. Amazonas.
         24. Leaf-blades 20 cm long, 3 mm wide, the inner ones white at base. Cerro Vinilla ..... 51.3. *N. berryana*
         24. Leaf-blades 6–12 cm long, 3–6 mm wide.
            25. Blades covered beneath with appressed white scales. Moriche ..... 52. *N. semiserrata*
            25. Blades laxly vestite beneath and on the margins with filamentous white trichomes. Neblina ..... 52.1. *N. filifera*
   20. Leaf-blades serrulate throughout, 4–10 cm long.
      26. Blades covered beneath with white appressed scales. Bolívar: Jáua ..... 50. *N. lasiantha*
      26. Blades soon glabrous on both sides.
         27. Floral bracts obtuse or apiculate; posterior sepals cucullate or obtuse.
            28. Blades with a median white stripe when dry, uniform; floral bracts and sepals membranaceous, transparent. Amazonas: Neblina ..... 50.1. *N. liesneri*
            28. Blades dimorphic, the inner ones basally pale.
               29. Floral bracts thickened at apex; posterior sepals cucullate. Bolívar: Guaiquinima ..... 47. *N. cucullata*
               29. Floral bracts uniformly membranaceous; posterior sepals obtuse. Amazonas: Cerro Vinilla ..... 47.1. *N. delascionis*
         27. Floral bracts acute; posterior sepals cucullate.
            30. Floral bracts thickened at apex. Bolívar.
               31. Leaf-blades abruptly acute. Jáua ..... 48. *N. intermedia*
               31. Leaf-blades evenly filiform-attenuate. Marutani ..... 48.1. *N. geaster*

30. Floral bracts uniformly thin.
    32. Lowest floral bracts serrulate near apex, red-brown; inner leaves not pale at base, leaf-blades 2.5 mm wide. Bolívar: Río Caura, Jáua ..... 46. *N. cardonae*
    32. Lowest floral bracts and all others entire, green; inner leaves pale at base.
        33. Floral bracts broadly elliptic, acute and mucronulate, about equaling the sepals; leaf-blades 3–5 mm wide. Amazonas: Neblina ..... 49. *N. abysmophila*
        33. Floral bracts ovate, acuminate, shorter than the sepals; leaf-blades 2.5 mm wide. Bolívar: Guaiquinema ..... 49.1. *N. emergens*

38.1. *Navia ovoidea* L. B. Smith, Steyermark & Robinson in Steyermark et al., Brittonia 33: 31, fig. 2C, D. 1981.

38.2. *Navia albiflora* L. B. Smith, Steyermark & Robinson in Steyermark et al., Acta Bot. Venez. 14(3): 11, figs. 8, 10f–h. 1984.

39.1. **Navia pedemontana** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 14, 29i–l. TYPE: Venezuela. Amazonas: Dept. Atabapo, orilla de una quebrada, vecinidad de la cominidad de Culebra, río Cunucunuma, 200–220 m alt., Lat. 3°40′N, Long. 65°45′W, 22–23, 28–29 March, 1–4 April 1983, *Julian A. Steyermark & Francisco Delascio 129063* (holotype, US; isotype, VEN).

Caulescens; caule sursum curvato, 10 cm longo. Folia ultra 3 dm longa; vaginis parvis, atris; laminis linearibus, 17 mm latis, apice attenuatis, ad basin versus paulo contractis, planis, mox glabris, serrulatis, siccis linea mediana pallida auctis.

Inflorescentia sessilis, e spicis 3 dense digitata; bracteis primariis subfoliaceis, inflorescentiam multo superantibus; spicis dense ovoideis, ea centrali 2 cm longa, lateralibus multo minoribus. Bracteae florigerae sepala subaequantes, late rotundatae apiculataeque. Sepala libera, 14 mm longa, posterioribus anguste oblongis, latere 1 mm latis, obtusis; petalis albis (Steyermark & Delascio); ovario supero.

Leaf anatomy. Vascular bundles mostly narrowly covered with chlorenchyma adaxially; adaxial water storage cells ca. 3-stratose; adaxial and abaxial subepidermal cells indistinct, not incrassate; substomatal cells with walls not thickened, with pairs of simple papillae projecting into pore on each side; scales peltate, slightly lobed, walls of cells indistinct.

On the basis of leaf-anatomy the new species falls closer to *N. semiserrata* than any near which it is placed in the key. None of the other species with complex inflorescences have such open substomatal pores with simple pairs of papillae. *Navia navicularis* and *N. breweri* differ further by having hairs rather than scales on the leaves.

Known only from the type.

39.2. *Navia jauana* L. B. Smith, Steyermark & Robinson in Steyermark & Brewer-Carías, Bol. Soc. Venez. Cienc. Nat. 22(132–133); 287, fig. 5. 1976.

39.3. *Navia luzuloides* L. B. Smith, Steyermark & Robinson in Steyermark & Brewer-Carías, Bol. Soc. Venez. Cienc. Nat. 22(132–133): 289, fig. 6. 1976.

39.4. *Navia scirpiflora* L. B. Smith, Steyermark & Robinson in Steyermark & Brewer-Carías, Bol. Soc. Venez. Cienc. Nat. 22(132–133): 307, fig. 7. 1976.

43.1. **Navia crassicaulis** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 15, 29m–s. TYPE: Venezuela. Amazonas: Dept. Río Negro, Camp III, Neblina and Massif, NW Plateau (arm), 13.5 km ENE of Cerro de La Neblina Base Camp, 1,750–1,850 m alt., Lat. 0°54′N, Long. 66°04′W, 16–18 February 1984, *Ronald Liesner 16026* (holotype, US; isotype, MO).

Caulescens; caule erecto, robusto, 30 cm alto. Folia 20 cm longa; vaginis brevibus, atris; laminis anguste triangularibus, 18 mm latis, utrinque trichomatibus subulatis fragilibus basi semiglobosis persistentibus laxe vestitis, laxe serrulatis.

Inflorescentia terminalis, sessilis; bracteis primariis foliaceis, inflorescentiam multo superantibus. Bracteae florigerae late obovatae, apice apiculatae serrulataeque. Sepala libera, posterioribus lanceolatis, obtusis, cuculatis, 10 mm longis; ovario supero.

Leaf anatomy. Vascular bundles adaxially maximally and abaxially minimally covered by chlorenchyma; water storage cells forming distinct abaxial canals; adaxial subepidermal cells in 3–4 layers, resiniferous, exterior cells in part with thickened walls; abaxial subepidermal cells resiniferous, unistratose; substomatal pores not occluded, oval; abaxial scales minute, peltate.

On the basis of leaf anatomy the species falls closest to such Colombian species as *Navia acaulis, N. bicolor,* and *N. heliophila,* which have connate sepals. The species placed close in the

above key all differ by having variously occluded substomatal pores, and most have no abaxial water storage canals.

Known only from the type.

43.2. **Navia linearis** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 16, 30a–e. TYPE: Venezuela. Amazonas: Dept. Atabapo, Cerro Marahuaca, shaded face of wet sandstone bluff, southwest-facing slopes, headwaters of Río Iguapo, southern sector of Meseta Sur-Este, 1,560 m alt., Lat. 3°36′00″N, Long. 65°23′10″W, 13–14 October 1983, *Julian A. Steyermark 129646* (holotype, US; isotype, VEN).

Caulescens; caule erecto, 10 cm alto. Folia 12 cm longa; vaginis brevibus; laminis linearibus, 9 mm latis, apice attenuatis, basi paulo contractis, utrinque trichomatibus subulatis fragilibus basi semiglobosis persistentibus laxe vestitis, laxe serrulatis.

Inflorescentia terminalis, sessilis, pauciflora; bracteis primariis subfoliaceis, inflorescentiam multo superantibus. Bracteae florigerae oblongae, obtusae, membranaceae, integrae. Sepala libera, posterioribus linearibus, obtusis, cucullatis, 10 mm longis; petalis albis (Steyermark); ovario supero.

Leaf anatomy. Vascular bundles narrowly covered by chlorenchyma adaxially and abaxially; subepidermal cells slightly differentiated, not incrassate; substomatal cells with walls not thickened, with pairs of commonly lobed or flexuous papillae protruding into pore on each side; scales minute, obsoletely peltate.

The combination of geography, floral characters in the key above, and the commonly lobed papillae of the substomatal pores would indicate closest relationship of the new species is to *Navia latifolia* and *N. cretacea.* The last two are distinguished by the cretaceous leaf undersurfaces.

Known only from the type.

47.1. **Navia delascionis** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 21, 31h–n. TYPE: Venezuela. Amazonas: Dept. Río Negro, in exposed drier places of savanna, on outcrops of quartzite, vicinity and northward from Cerro Vinilla, 440–600 m alt., Lat. 2°31′N, Long. 65°23′W, 1–2 March 1984, *Steyermark, Berry & Delascio 130410* (holotype, US; isotype, VEN).

Caulescens; caule erecto, 8 cm alto. Folia 10 cm longa; vaginis parvis, atris; laminis anguste triangularibus, 3 mm latis, albo-ciliatis, alibi mox glabris, laxe serrulatis, interioribus ad basin versus albis.

Inflorescentia terminalis, sessilis, anguste ovoidea, 2 cm alta, atrocastanea; bracteis primariis subfoliaceis, inflorescentiam superantibus. Bracteae florigerae ellipticae, quam sepalis paulo breviores, membranaceae, rubro-brunneae. Sepala libera, posterioribus linearibus, obtusis, 10 mm longis; ovario supero.

Leaf anatomy. Vascular bundles covered by chlorenchyma adaxially and abaxially; the innermost adaxial water storage cells sporadically resiniferous; subepidermal cells mostly unistratose, abaxially mostly resiniferous; substomatal pores nearly occluded, transversely elongate, halteriform; abaxial scales not evident.

The new species seems rather distinct among those with nearly occluded substomatal pores by the broad covering of chlorenchyma adaxially over the vascular bundles. Of the species placed close in the above key, relationship is perhaps closest to some from western Bolívar such as *Navia lasiantha* and *N. cardonae.*

Known only from the type.

48.1. *Navia geaster* L. B. Smith, Steyermark & Robinson in Steyermark et al., Acta Bot. Venez. 14(3): 14, fig. 2j–p. 1984.

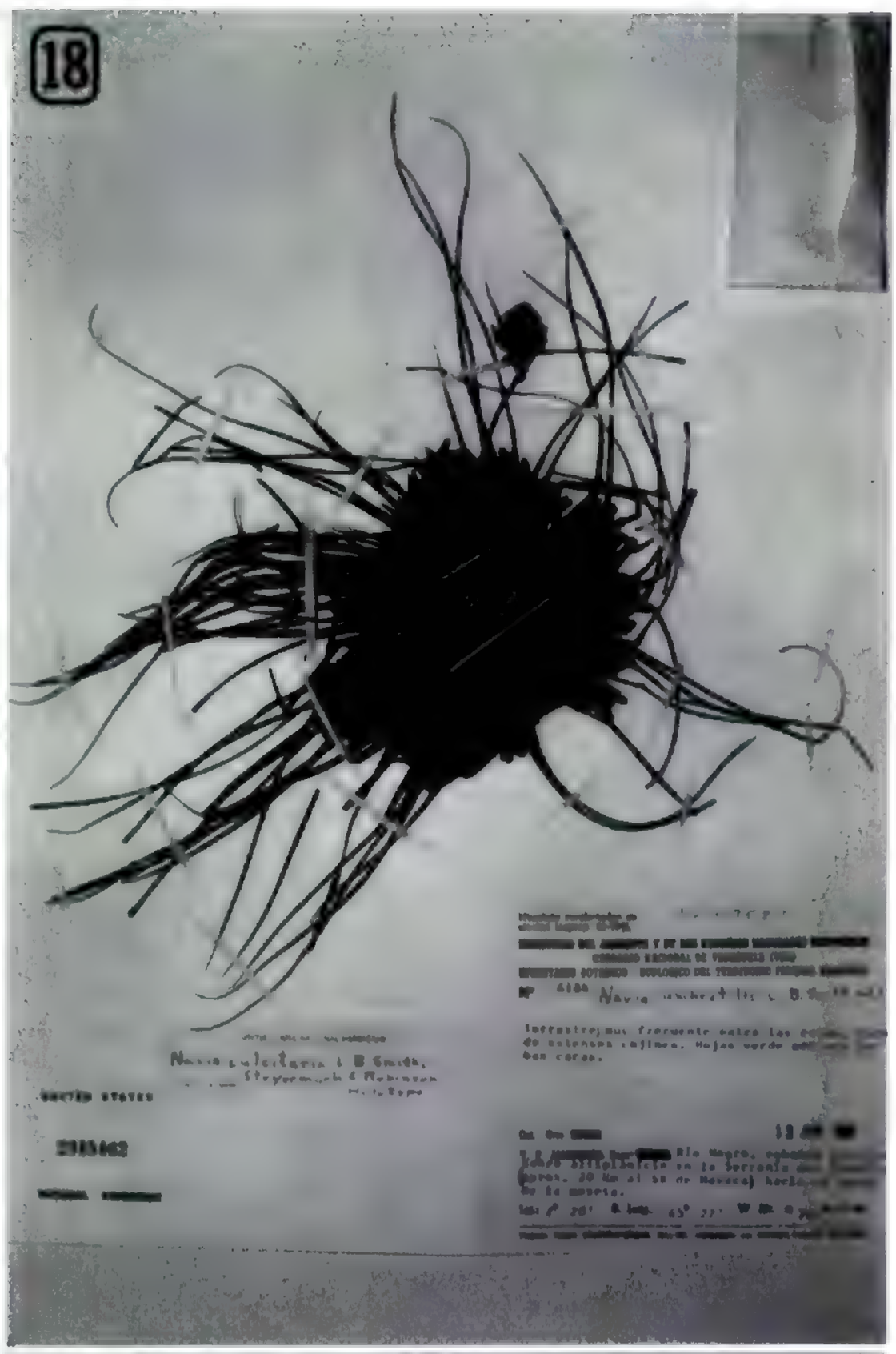
49.1. *Navia emergens* L. B. Smith, Steyermark & Robinson in Steyermark et al., Brittonia 33: 31, fig. 2A, B. 1981.

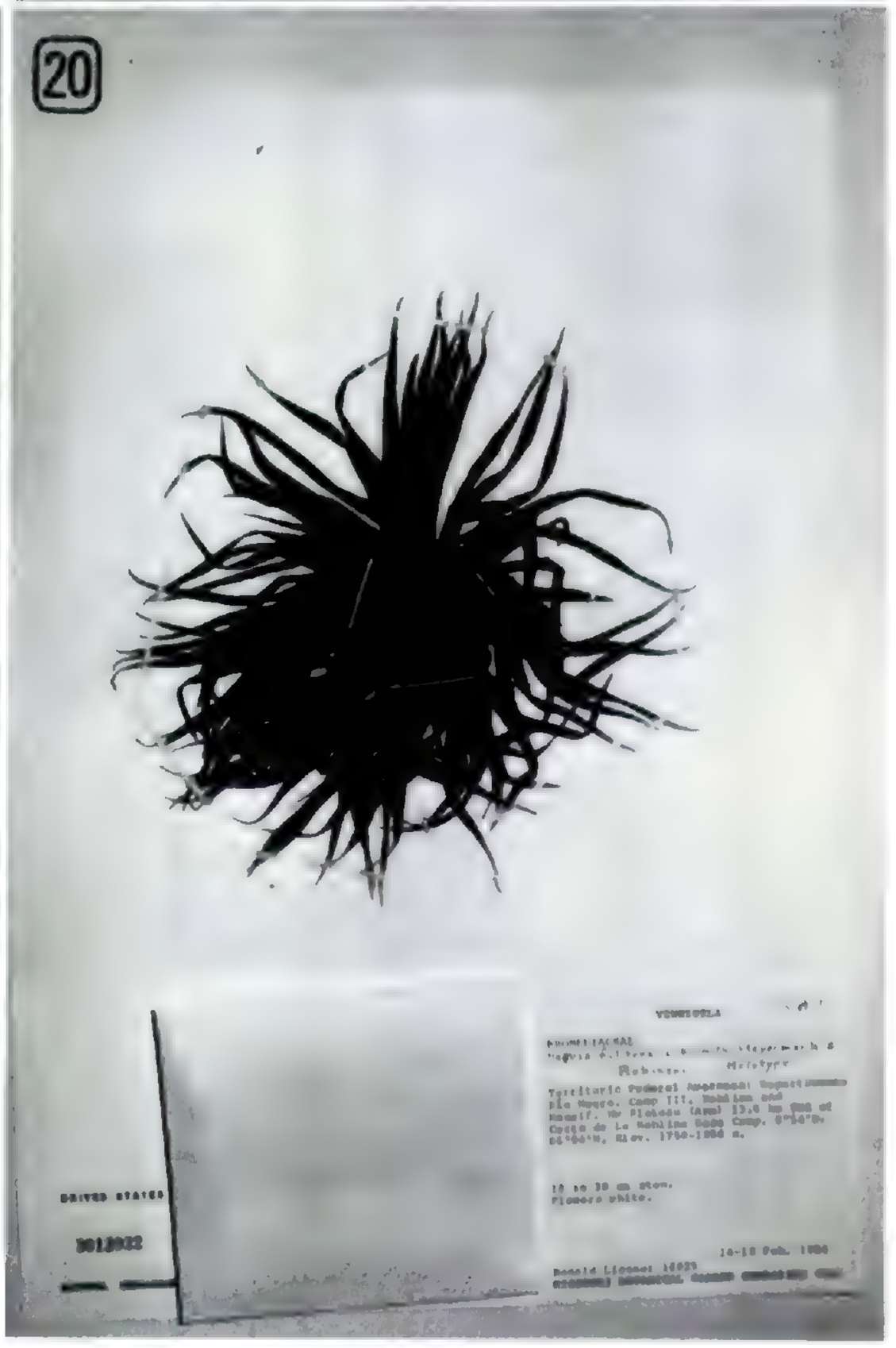
50.1. **Navia liesneri** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 21, 31a–g. TYPE: Venezuela. Amazonas: Dept. Río Negro, Cerro de Neblina, Puerto Chimo Camp on Río Mawarinuma and up north slope of canyon, 150–1,800 m alt., Lat. 00°50′N, Long. 66°07′W, 11 February 1984, *Ronald Liesner & Charles Brewer 15866* (holotype, US; isotype, MO).

Caulescens; caule erecto, ca. 11 cm alto. Folia 7 cm longa; vaginis parvis, a laminis omnino occultis; laminis anguste triangularibus, 4 mm latis, siccis linea mediana alba auctis aliter uniformibus, alto-ciliatis, alibi glabris, laxe serrulatis.

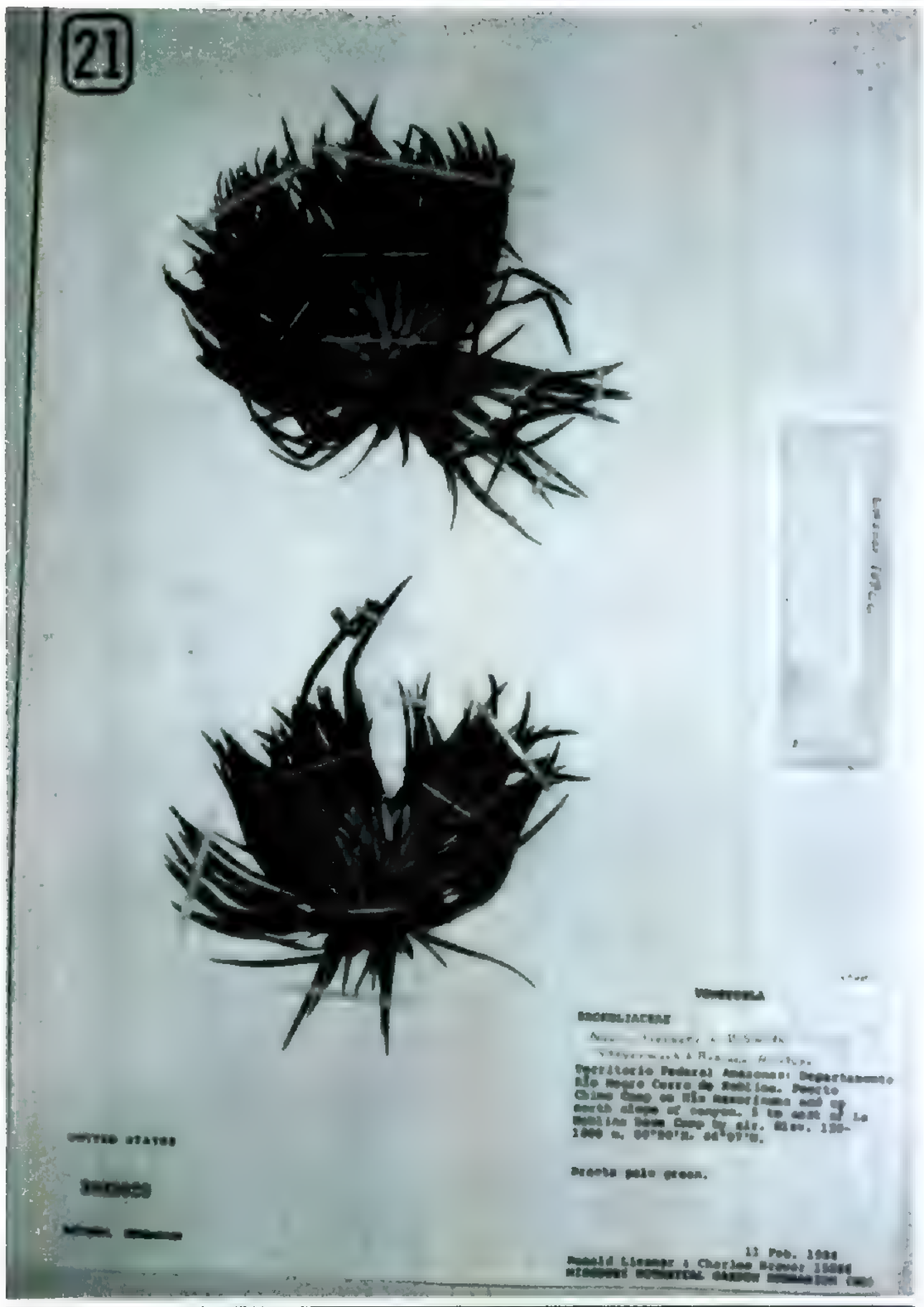
Inflorescentia terminalis, sessilis, subglobosa, 12 mm diametro; bracteis involucrantibus foliaceis, inflorescentiam superantibus. Bracteae florigerae ellipticae, obtusae, sepala subaequantes, membranaceae, transparentes. Sepala libera, posterioribus linearibus, obtusis, 9 mm longis; ovario supero.

Leaf anatomy. Vascular bundles not or scarcely covered by chlorenchyma adaxially and abaxially; water storage cells forming slightly distinct abaxial canals; subepidermal cells incrassate, unistratose; substomatal pores not occlud-





FIGURES 17–20.—17. *Navia piresii* Smith, Steyermark & Robinson.—18. *Navia culcitaria* Smith, Steyermark & Robinson.—19. *Navia berryana* Smith, Steyermark & Robinson.—20. *Navia filifera* Smith, Steyermark & Robinson.



FIGURES 21–24.—21. *Navia liesneri* Smith, Steyermark & Robinson.—22. *Navia delascionis* Smith, Steyermark & Robinson.—23. *Navia igneosicola* Smith, Steyermark & Robinson.—24. *Brewcaria marahuacae* Smith, Steyermark & Robinson.

ed, rounded or oval; abaxial scales small, peltate, lobed, with cells indistinctly oblong.

The leaf anatomy, with the vascular bundles exposed both dorsally and ventrally to water storage tissue, and substomatal pores without intrusions, is a combination commonly seen in *Lindmania,* but such a combination distinguishes the new species from all previously known species of *Navia.* All the features of the new species, however, are found independently in various species of *Navia* and the combination was to be expected in the genus. The non-occluded substomatal pores alone distinguish the species from all others placed with it in the above key on the basis of having the leaf-blades serrulate throughout.

Known only from the type.

51.1. **Navia culcitaria** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 18, 30l–o. TYPE: Venezuela. Amazonas: Dept. Río Negro, sabanas abiertas sobre altiplanicie en la Serranía del Vinilla (ca. 20 km al SW de Mavaca) hacia el borde SW de la meseta, terrestre; muy frecuente entre las rocas, formando extensos cojines, 760 m alt., Lat. 2°20′, Long. 65°22′, 13 June 1981, *O. Huber 6184* (holotype, US; isotype, VEN).

Herba pulvinos extensos formans (Huber), caulescens caule brevissimo. Folia plurima, ad 17 cm longa; laminis sublinearibus, vulgo 3 mm raro 5 mm latis, integris, margine albo-ciliatis, alibi glabris.

Inflorescentia sessilis, ovoidea, multiflora; bracteis involucrantibus foliaceis. Bracteae florigerae ellipticae, apiculatae, quam sepalis breviora. Sepala libera, anguste oblonga, obtusa, cucullata, 11 mm longa.

Leaf anatomy. Vascular bundles broadly covered by chlorenchyma adaxially and abaxially; water storage cells only adaxial, up to 4-stratose; subepidermal cells of both surfaces narrow, scarcely incrassate; substomatal pores nearly occluded, transversely elongate, halteriform, with walls strongly thickened.

In its leaf anatomy the species seems close to *Navia cardonae* and the above described *N. delascionis* both of which differ by their shorter more serrulate leaves.

Known only from the type.

51.2. **Navia piresii** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 18, 30f. TYPE: Brazil. Amazonas: Serra Aracá, 10 February 1975, *J. M. Pires 15.014 (37) (holotype, US; isotype, IPEAN).*

Caulescens; caule qui adest brevissimo. Folia ad 15 cm longa; vaginis brevibus, ovatis, atro-castaneis; laminis angustissime triangularibus, 5 mm latis, integris, marginibus albo-ciliatis, alibi glabris.

Inflorescentia sessilis, pauciflora; bracteis involucrantibus ellipticis, apiculatis, inflorescentiam aequantibus, tenuibus, siccis rubro-brunneis. Bracteae florigerae anguste ellipticae, sepala aequantes, membranaceae. Sepala libera, oblonga, obtusa, 10 mm longa.

Leaf anatomy. Vascular bundles broadly covered by chlorenchyma adaxially and abaxially; water storage cells adaxially up to 5-stratose, abaxially less inflated, indistinctly demarcated, ca. 3-stratose; subepidermal cells on both surfaces narrow, scarcely incrassate; substomatal pores broadly oval, with slight paired protrusions on each side at junctures of cells, with walls not incrassate; abaxially only obconical basal parts of scales seen.

In size and anatomy the leaf of the species seems close to the Colombian species, *Navia bicolor,* which belongs to a distinct group having connate sepals. The abaxial water storage tissue is not as prominent, being more like a pale, more enlarged abaxial zone of the chlorenchyma. Perhaps closest relationship is to the above described *N. crassicaulis,* which is distinguished by its broader leaves and generally more robust stature.

Known only from the type.

51.3. **Navia berryana** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 19, 30g–k. TYPE: Venezuela. Amazonas: Dept. Río Negro, on rocks along stream, on outcrops of quartzite in savannas and gallery forests near and north of Cerro Vinilla, ca. 30 km SSW from Ocamo, along streams tributary to the Río Orinoco, 440–600 m alt., Lat. 2°31′N, Long. 65°23′W, 1–2 March 1984, *Steyermark, Berry & Delascio 130318-A* (holotype, US; isotype, VEN).

Caulescens; caule erecto, 4 cm alto. Folia 20 cm longa; vaginis brevibus; laminis angustissime triangularibus, 3 mm latis, marginibus ciliatis alibi glabris, minutissime laxeque serrulatis, interioribus basi albis.

Inflorescentia terminalis, breviter scaposa; scapi bracteis foliaceis. Bracteae florigerae late rotundae, apice apiculatae incrassataeque. Sepala libera, 9 mm longa, lateralibus linearibus, apice apiculata incrassataque.

Leaf anatomy. Vascular bundles covered by

chlorenchyma adaxially and abaxially; innermost adaxial water storage cells sporadically resiniferous; subepidermal cells with parts of walls nearest leaf surface thickened, resiniferous; substomatal pores nearly occluded, transversely elongate, halteriform; abaxial scales sparse, rudimentary.

In the combination of its leaf anatomy and geography, the new species may be most closely related to *Navia delascionis* described above. The latter differs by its longer more serrulate leaves.

Known only from the type.

52.1. **Navia filifera** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 20, 30p–u. TYPE: Venezuela. Amazonas: Dept. Río Negro, Camp III, Neblina and Massif, NW Plateau (Arm), 13.5 km ENE of Cerro de La Neblina Base Camp, 1,750–1,850 m alt., Lat. 0°54′N, Long. 66°04′W, 16–18 February 1984, *Ronald Liesner 16025* (holotype, US; isotype, MO).

Caulescens; caule erecto, ca. 9 cm alto. Folia 12 cm longa; vaginis brevibus, atris; laminis anguste triangularibus, 6 mm latis, subtus et in marginibus trichomatibus filiformibus albis laxe vestitis, laxe serrulatis.

Inflorescentia terminalis, sessilis, subglobosa, 2 cm diametro, petalis exceptis trichomatibus filiformibus laxe vestita; bracteis involucrantibus subfoliaceis, inflorescentiam multo superantibus. Bracteae florigerae ovatae, acutae, valde nervatae, sepala subaequantes. Sepala libera, 7 mm longa; posterioribus obtusis cucullatisque; petalis albis (Liesner); ovario supero.

Leaf anatomy. Vascular bundles adaxially maximally and abaxially minimally covered by chlorenchyma; water storage cells forming strongly distinct abaxial canals; adaxial cells paucistratose; adaxial subepidermal cells 1–3-stratose, resiniferous, outermost with cell walls nearest leaf surfaces thickened; substomatal pores not occluded, rounded; abaxial hairs uniseriate, long, from bulbous base.

The leaf cross-section and the uniseriate hairs suggest closest relationship of the new species to *Navia crispa, N. viridis, N. lanigera,* and *N. myriantha,* all of which fall under Subkey II because of their more pointed, non-cucullate sepals.

Known only from the type.

REVISED SECTION OF SUBKEY IV

9. Leaf-blades not narrowed toward base; stems simple.
   9a. Posterior sepals 10 mm long, ½ connate; leaf-blades 1–2 mm wide. Cerro Sipapo ..... 60. *N. ocellata*
   9a. Posterior sepals 15 mm long, over ¾ connate, leaf-blades 4 mm wide. Cerro Sipapo ..... 60.1. *N. lactea*

60.1. *Navia lactea* L. B. Smith, Steyermark & Robinson in Steyermark et al., Acta Bot. Venez. 14(3): 14, fig. 5. 1984.

At the time of the original description, the species was noted as having separate sepals, but they were correctly illustrated as connate.

REVISED SECTION OF SUBKEY V

1. Leaf-blades 17–30(–35) mm wide; petals yellow; ovary partly or wholly inferior.
   1a. Stem very short; leaf-blades uniform, slightly contracted toward base, uniformly spinose-serrate. Bolívar, Guyana ..... 68. *N. arida*
   1a. Stem over 17 cm long; leaf-blades dimorphic, the terminal ones 40 cm long, 35 mm wide, flexible, adapted to shade, entire except for minute spines toward base, the lower blades grading to narrowly triangular, 6 cm long, uniformly narrowly triangular. Amazonas ..... 68.1. *N. igneosicola*

68.1. **Navia igneosicola** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 23, 31o–t. TYPE: Venezuela. Amazonas: Dept. Atures, area de selva y lajas igneas á lo largo del Río Coromoto, á Tobogán de la Selva, 35 km sureste de Puerto Ayacucho, 150 m alt., Lat. 5°22′N, Long. 67°33′W, 14 Mayo 1980, *Julian A. Steyermark, Gerrit Davidse & Francisco Guanchez 122478* (holotype, US; isotypes, NY, VEN).

Caulescens; caule curvato, ultra 17 cm longa. Foliorum vaginae parvae, inconspicuae; laminis dimorphis, eis terminalibus linearibus, apice attenuatis, ad basin versus paulo contractis et spinoso-serrulatis, 40 cm longis, 35 mm latis, flexibilibus et umbras amantibus, eis inferioribus mutatis in anguste triangularibus, ad basin versus haud contractis, omnino spinoso-serrulatis, 6 cm longis.

Inflorescentia centralis, sessilis, pauciflora; bracteis exterioribus ellipticis, tenuibus, foliaceo laminatis. Bracteae florigerae angustissime triangulares, 27 mm longae, sepalis superatae, integrae, membranaceae, albolepidotae. Sepala libera angustissime triangularia, ad 45 mm longa, tenuia; petalis aurantiacis (Steyermark); ovario fere vel omnino infero.

Leaf anatomy. Vascular bundles lacking a cover of chlorenchyma on all adaxial surfaces

and most abaxial surfaces, largest bundles with fiber sheaths extending nearly or completely to the epidermis adaxially and abaxially; water storage cells with only 2–3 layers; subepidermal cells not thickened on either surface; substomatal pores not occluded, rounded or oval; abaxial scales rounded, peltate, with cells distinct, subisodiametrical, irregularly disposed, peripheral cells smaller and more tenuous.

Navia igneosicola is evidently closely related to *N. arida,* showing the same type of leaf-section, substomatal pores, and distinctive scales on the leaves.

11.1. **BREWCARIA** L. B. Smith, Steyermark & Robinson in Steyermark et al., Acta Bot. Venez. 14(3): 10. 1984.

Plants with leaves fasciculate-rosulate, rigid, spinose-serrate, in cross-section with vascular bundles not covered with chlorenchyma adaxially, with chlorenchyma continuous and unusually dense abaxially, substomatal pores nearly occluded; inflorescence erect, simple, densely spicate; flowers sessile, spreading; sepals imbricate, ecarinate; petals regular, appendaged with 2 horizontally attached scales; stamens equal; ovary partly inferior, style branches narrowly oblong; seeds exappendiculate or very narrowly winged.

The genus is known only from central Amazonas in Venezuela. Closest relationship is evidently to *Navia,* from which it differs by its simple, densely spicate inflorescence and its appendaged petals. The appendages differ from those in the more distantly related *Steyerbromelia* by being transversely inserted.

1. Plant 2.5–3 m high; leaves more than 1 m long; blades lustrous beneath and sparsely lepidote, 25 mm wide; inflorescence 70 cm long ..... 1. *B. duidensis*
1. Plant not over 0.6 m high; leaves not over 0.5 m long; blades densely appressed lepidote beneath, 15 mm wide; inflorescence 16 cm long ..... 2. *B. marahuacae*

1. *Brewcaria duidensis* L. B. Smith, Steyermark & Robinson in Steyermark et al., Acta Bot. Venez. 14(3): 10, figs. 1a–j, 6a–e, photo 2. 1984.

2. **Brewcaria marahuacae** L. B. Smith, Steyermark & Robinson, sp. nov. Figures 24, 31u–y. TYPE: Venezuela. Amazonas: Dept. Atabapo, Cerro Marahuaca–Atuhua–Shiho, cumbre, parte aislada al Sur-Oeste del Cerro, vegetacion no arbolada en terreno pendiente terrestrial, common, 2,480 m alt., Lat. 3°30′N, Long. 65°20′W, 9–10 Feb. 1982, *J. A. Steyermark, M. Guariglia, N. Holmgren, J. Luteyn & Scott Mori 126328* (holotype, US; isotypes, NY, VEN). PARATYPES: Dept. Atabapo: Cerro Marahuaca–Huha, 31 Jan. 1982, *Steyermark, Guariglia, Holmgren, Luteyn & Mori 125909* (NY, US, VEN). Plant over 0.6 m high. Cerro Marahuaca, 10–12 Oct. 1983, *Steyermark 129519* (NY, US, VEN). Stem varnished as well as young inflorescence. Cerro Marahuaca, March 1984, *Ostos in Tamayo 6022* (VEN). Petals elliptic, cucullate, bearing 2 truncate scales.

Acaulis florigera usque 0.5 m alta. Folia multa, supremis usque 0.5 m longis; vaginis suborbicularibus, ca. 2 cm latis, subtus lepidotis; laminis angustissime triangularibus, basi 15 mm latis, planis, rigidis, spinis sursum curvatis 1 mm longis laxe serratis, supra dissite lepidotis, subtus squamis adpressis cinereis dense vestitis.

Scapus erectus, 13 mm diametro; scapi bracteis erectis, inferioribus foliaceis, dense imbricatis, superioribus ovatis, acuminatis, internodia superantibus sedscapum haud omnino occultantibus. Inflorescencia spica densa, multiflora, 16 cm longa. Bracteae florigerae late ovatae, acuminatae, sepala subaequantes; floribus sessilibus, patentibus. Sepala ovata, obtusa, fructificantia 10 mm longa, posteriora obtuse carinata, cucullata. Ovarium paulo inferum. Semina angustissime alata.

Leaf anatomy. Scarcely distinct from *Brewcaria duidensis,* but with less enlarged chlorenchyma cells between the vascular strands, and with raphid-bearing idioblasts between most of the strands.

The cited differences in the leaf anatomy are based on a limited sample and should be used with caution.

TILLANDSIOIDEAE

14. **TILLANDSIA** L. Sp. Pl. 286. 1753.

REVISED SECTION OF SUBKEY IX

46a. Plant flowering 1–2 m high; primary bracts lanceolate, acute. Colombia, Ecuador, Peru ..... 9. *T. pyramidata*
46a. Plant flowering ca. 0.6 m high; lower primary bracts linear-laminate. Venezuela ..... 9.1. *T. abysmophila*

9.1. **Tillandsia abysmophila** L. B. Smith & Steyermark, sp. nov. Figures 25, 32a–d. TYPE:

FIGURES 25, 26.—25. *Tillandsia abysmophila* Smith & Steyermark.—26. *Guzmania terrestris* Smith & Steyermark.

Venezuela. Amazonas: Dept. Río Negro, Cerro Aratitiyope, epifita en selva alta, a lo largo de un riachuelo afluente a Río Manipitare, 990–1,670 m alt., Lat. 2°10′N, *Julian A. Steyermark, Paul Berry & Francisco Delascio 130135* (holotype, US; isotypes, NY, VEN).

Verisimiliter acaulis, florifera ca. 6 dm alta. Folia ca. 5 dm longa, subtus squamis adpressis cinereis in centro atris dense vestita; vaginis ellipticis, 10 cm longis, supra lepidotis; laminis ligulatis, acuminatis, 3 cm latis, supra glabris.

Scapus erectus, gracilis; scapi bracteis subfoliaceis, dense imbricatis. Inflorescentia laxe bipinnatim paniculata, 26 cm longa, glabra; bracteis primariis late ovatis, quam spicis brevioribus, inferioribus linearilaminatis; spicis divergentibus, sessilibus, lineari-lanceolatis, 8.5 cm longis, 1.5 cm latis, complanatis. Bracteae florigerae ovatae, acutae, 25 mm longae, carinatae, rigidae, laevigatae. Sepala linearia, acuta, 22 mm longa, bracteis florigeris inclusa, posteriora carinata, alte connata.

16. **GUZMANIA** Ruiz & Pavon, Fl. Peruv. Chil. 3: 37, pl. 266. 1802.

REVISED SECTION OF KEY

36a. Floral bracts 15 mm long, their margins broad, pale, strongly crisped; sepals 31 mm long, similar to the floral bracts. Colombia ..... 28. *G. radiata*

36a. Floral bracts 10 mm long, concolorous, their margins scarcely if at all crisped. Venezuela ..... 28.1. *G. terrestris*

28.1. **Guzmania terrestris** L. B. Smith & Steyermark sp. nov. Figures 26, 32e–l. TYPE: Venezuela. Amazonas: Dept. Atabapo, Cerro Marahuaca, Cumbre, parte central de la Meseta Sur-Este, al lado de una grieta, a lo largo de la Quebrada Yekuana, afluente del Río Negro, 2,560 m alt., Lat. 3°40′30″N, Long. 65°26′20″O, 10–12 Oct. 1983, *Julian A. Steyermark 129596* (holotype, US; isotypes, NY, VEN). PARATYPE: Cerro Marahuaca, 13–14 Oct., *Steyermark 129526* (NY, US, VEN).

Verisimiliter acaulis, florigera ultra 47 cm alta. Folia 35 cm longa, utrinque squamis minimis dissite lepi-

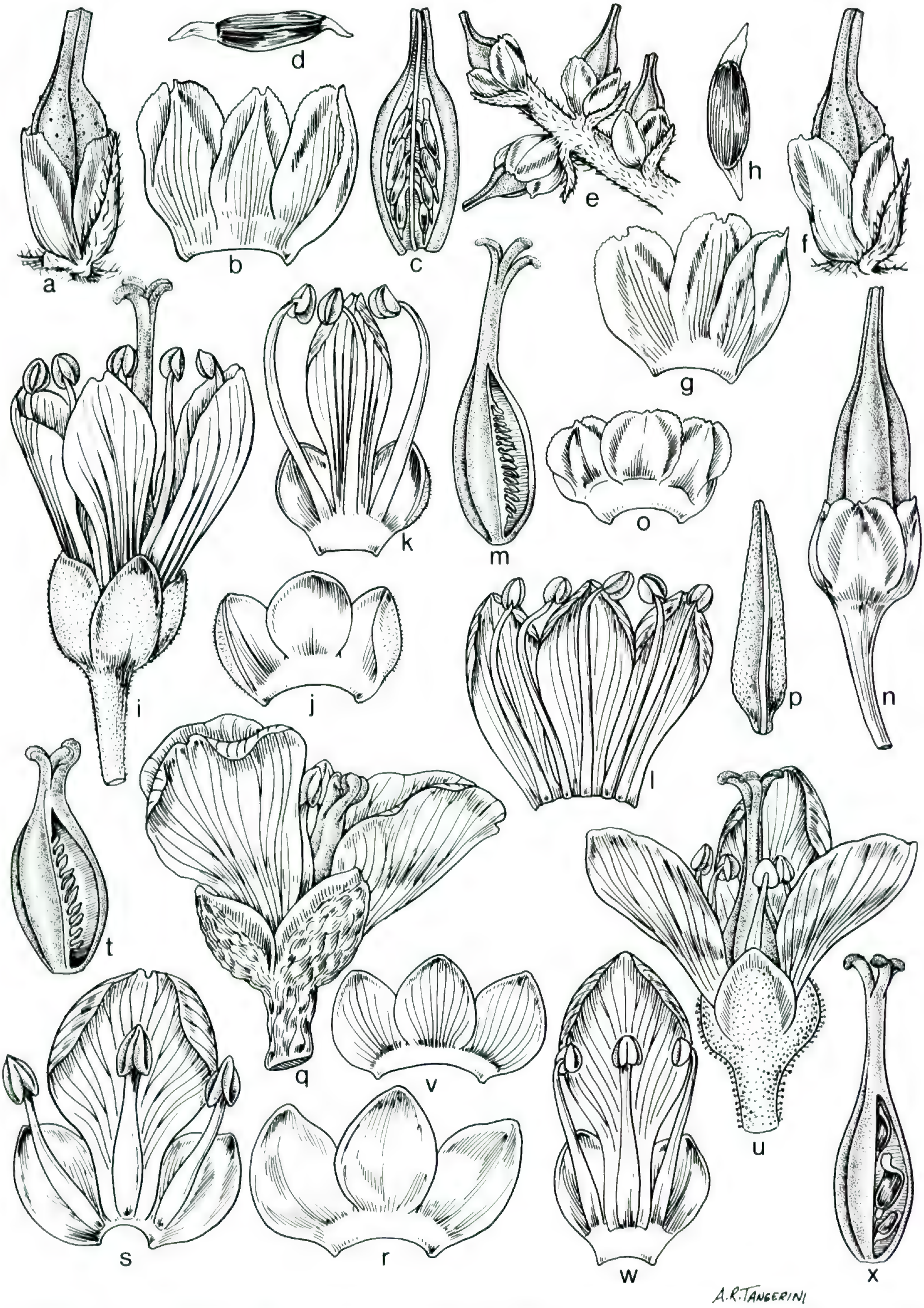


FIGURE 27.—a. *Lindmania sessilis* flower.—b. Sepals.—c. Fruit.—d. Seed.—e. *Lindmania saxicola* branch of inflorescence.—f. Flower.—g. Sepals.—h. Seed.—i. *Lindmania aurea* flower.—j. Sepals.—k. Petals, stamens and sepals.—l. Petals.—m. Pistil.—n. *Lindmania imitans* flower.—o. Sepals.—p. Seed.—q. *Lindmania riparia* flower.—r. Sepals.—s. Petals and stamens.—t. Pistil.—u. *Lindmania piresii* flower.—v. Sepals.—w. Petal and stamens.—x. Pistil.

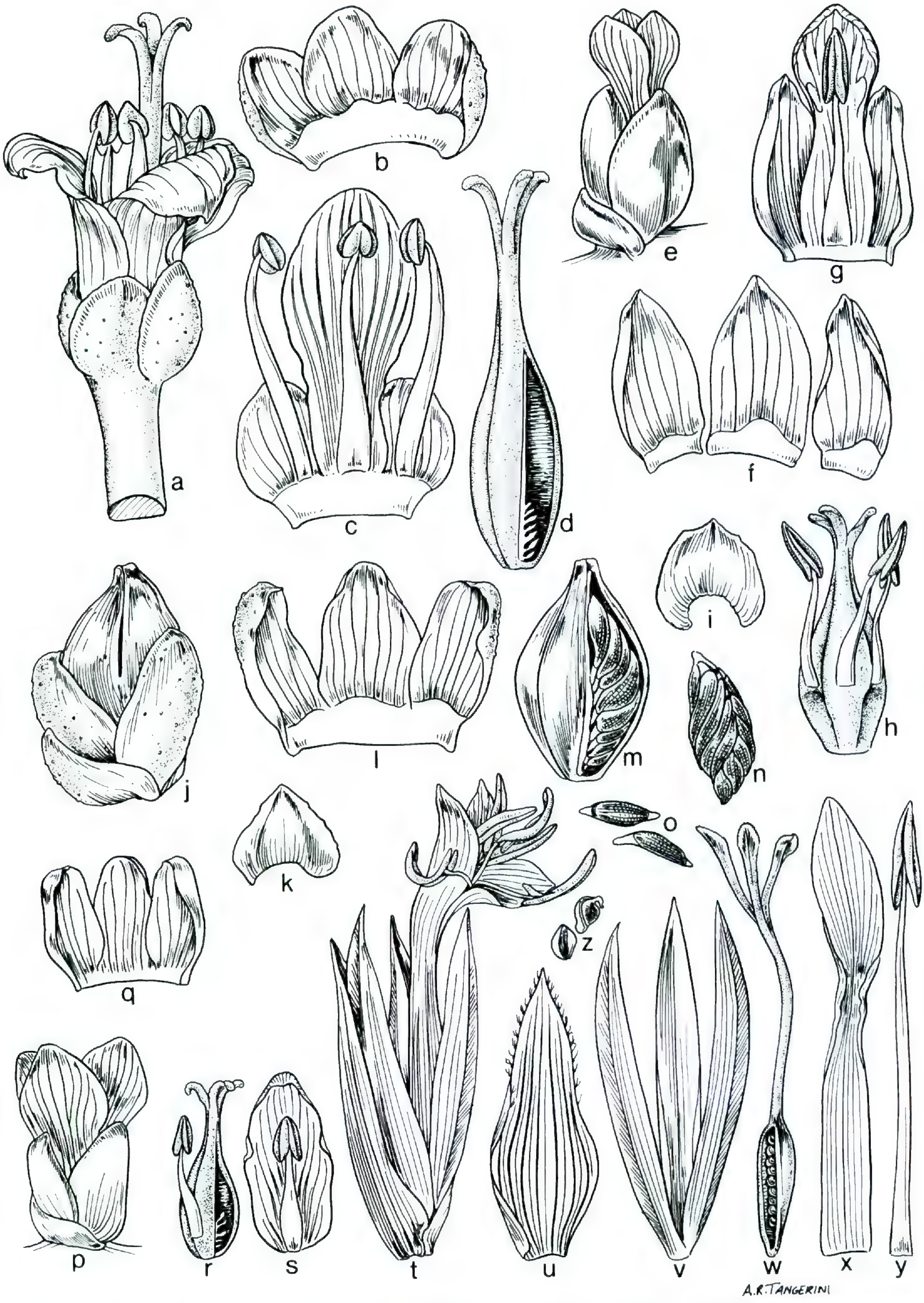


FIGURE 28.—a. *Lindmania huberi* flower.—b. Sepals.—c. Petals and stamens.—d. Pistil.—e. *Steyerbromelia diffusa* flower.—f. Sepals.—g. Appendaged petals and stamens.—h. Pistil and stamens.—i. Bract.—j. *Navia plowmanii* flower.—k. Bract.—l. Sepals.—m. Ovary.—n. Seed cluster.—o. Seeds.—p. *Navia thomasii* flower.—q. Sepals.—r. Pistil and stamens.—s. Petal and stamen.—t. *Navia polyglomerata* flower.—u. Bract.—v. Sepals.—w. Pistil.—x. Petal.—y. Stamen.—z. Seeds.

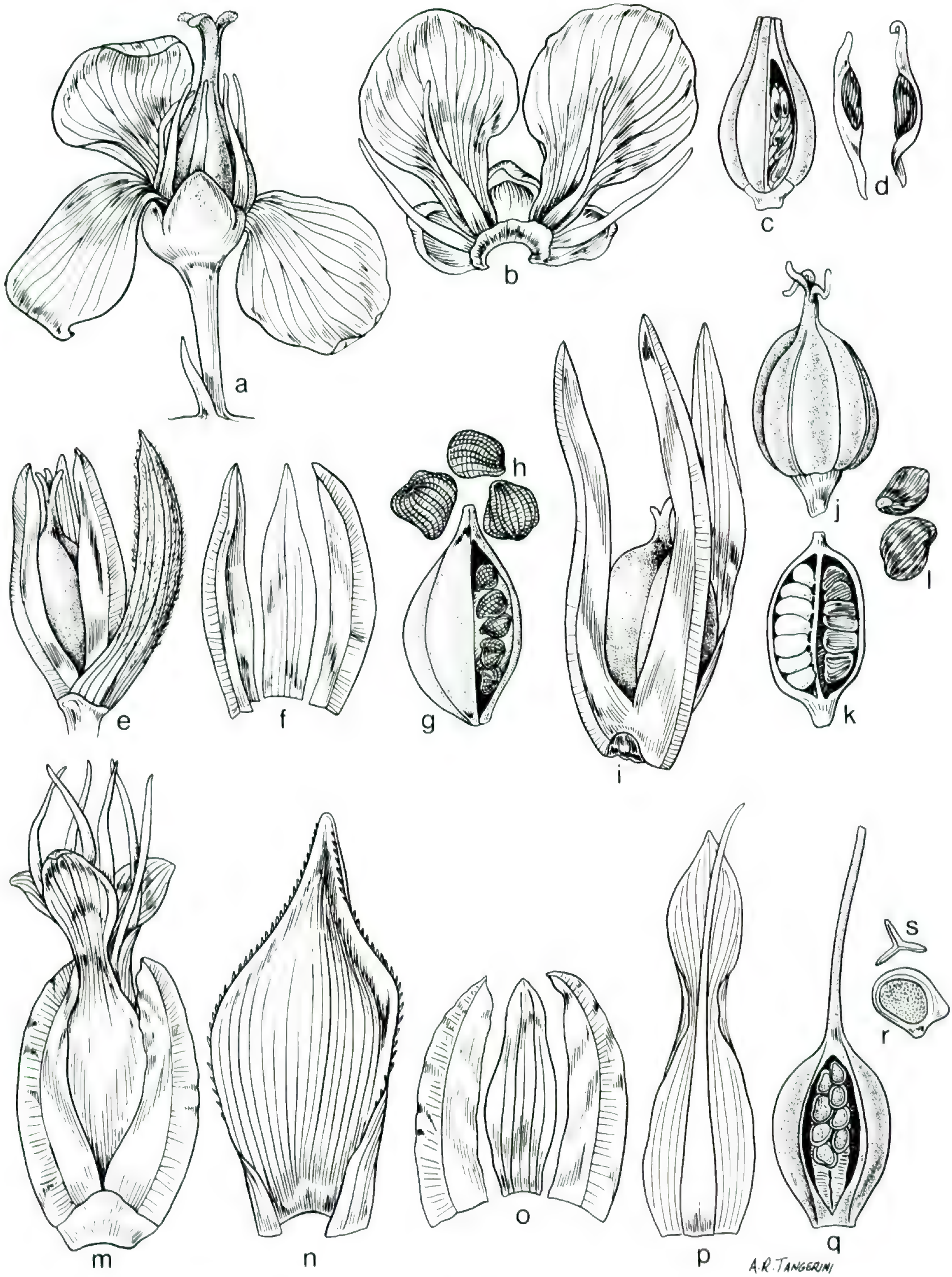


FIGURE 29.—a. *Lindmania terramarae* flower and bract.—b. Sepals and petals.—c. Fruit and seeds.—d. Seeds.—e. *Navia huberiana* flower and bract.—f. Sepals.—g. Fruit.—h. Seeds. i. *Navia pedemontana* sepals and fruit.—j. Fruit.—k. Fruit showing seeds.—l. Seeds.—m. *Navia crassicaulis* flower.—n. Bract.—o. Sepals.—p. Petal and filament.—q. Fruit showing seeds.—r. Seed.—s. Section of ovary (orange part).

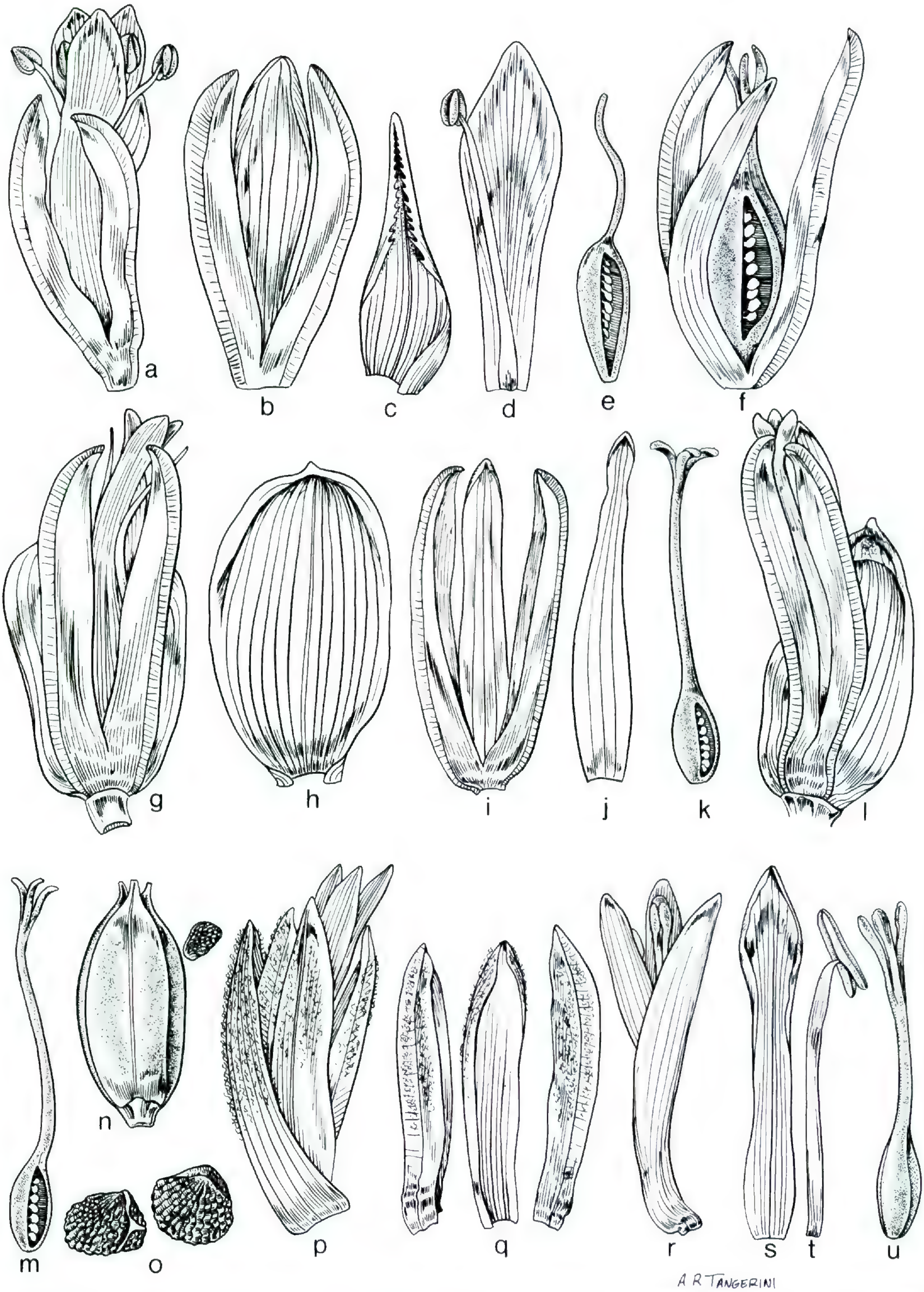


FIGURE 30.—a. *Navia linearis* flower.—b. Sepals.—c. Bract.—d. Petal and stamen.—e. Pistil.—f. *Navia piresii* sepals and pistil.—g. *Navia berryana* flower and bract.—h. Bract.—i. Sepals.—j. Petal.—k. Pistil.—l. *Navia culcitaria* flower and bract.—m. Pistil.—n. Fruit and seed.—o. Seeds.—p. *Navia filifera* flower and bract.—q. Sepals.—r. Petals.—s. Petal.—t. Stamen.—u. Pistil.

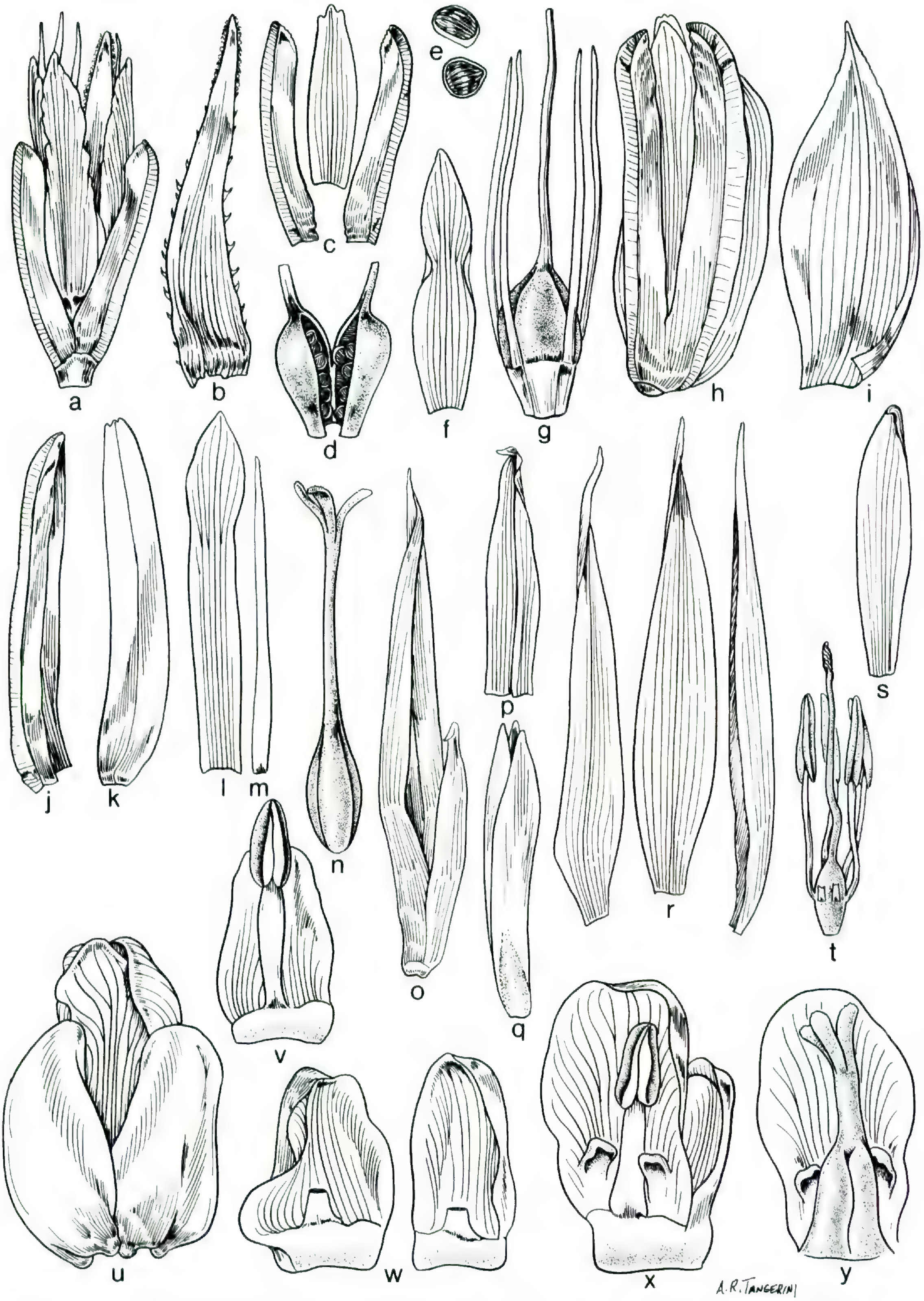


FIGURE 31.—a. *Navia liesneri* flower.—b. Bract.—c. Sepals.—d. Ovary and seeds.—e. Seeds.—f. Petal.—g. Pistil and filaments.—h. *Navia delascionis* sepals and bract.—i. Bract.—j. Posterior sepal.—k. Anterior sepal.—l. Petal.—m. Filament.—n. Pistil.—o. *Navia igneosicola* flower and bract.—p. Bract.—q. Flower.—r. Sepals.—s. Petal.—t. Pistil and stamens.—u. *Brewcaria marahuacae* flower.—v. Sepal and stamen.—w. Sepals.—x. Sepal, petal and stamen.—y. Petal and pistil.

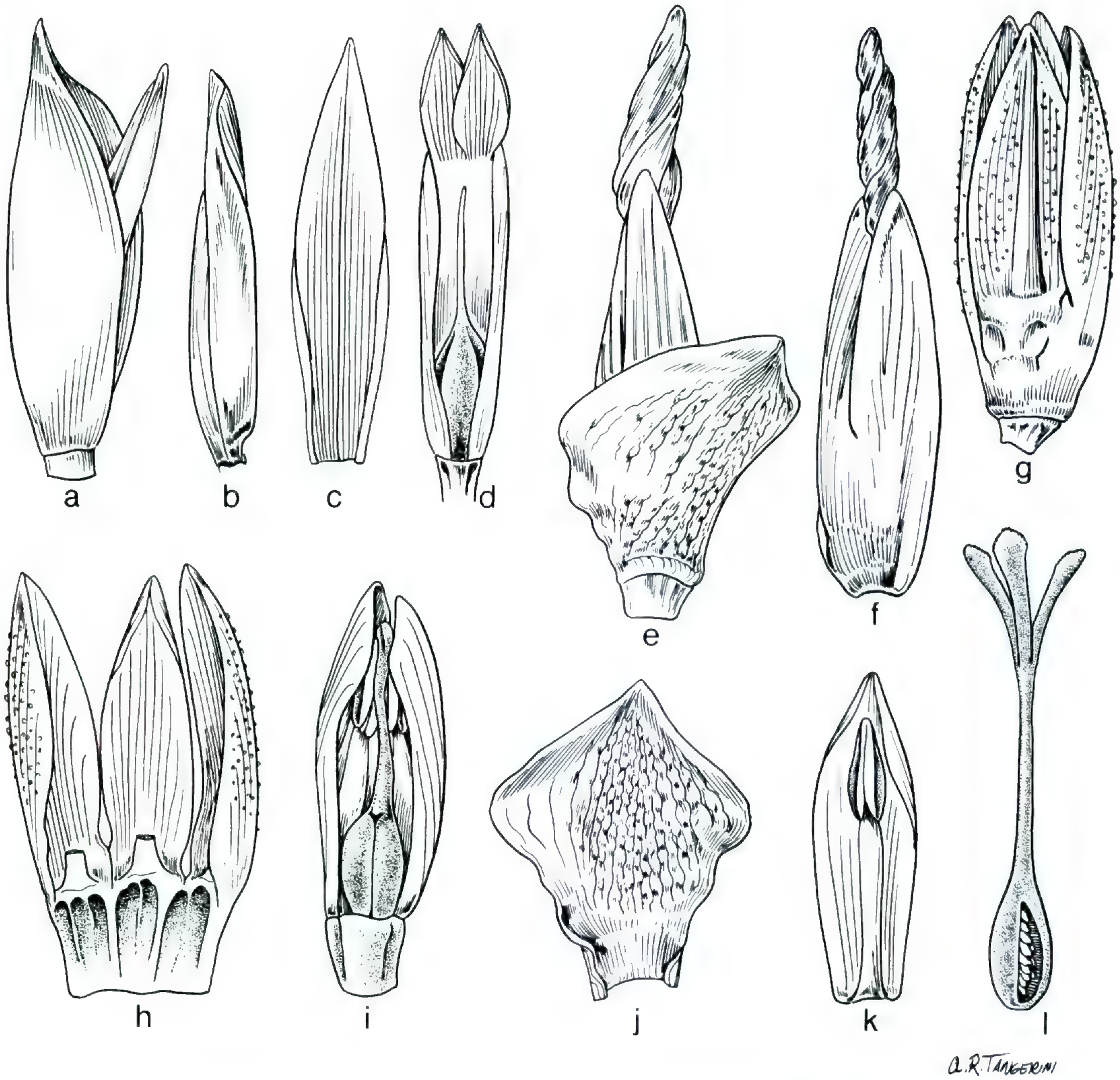


FIGURE 32.—a. *Tillandsia abysmophila* bract and flower.—b. Sepals closed.—c. Anterior sepal.—d. Posterior sepals.—e. *Guzmania terrestris* flower and bract.—f. Flower.—g. Sepals.—h. Sepals opened.—i. Petals, stamens and pistil.—j. Bract.—k. Petal and stamen.—l. Pistil and ovules.

dota; vaginis brevibus amplis; laminis anguste oblongis, 4 cm latis, apice attenuatis.

Scapus cylindricus, obscure lepidotus; scapi bracteis erectis, imbricatis, late ovatis, attenuatis. Inflorescentia laxe bipinnatim paniculata, 38 cm longa, dissite lepidota, mox glabra; bracteis primariis ovatis, infimis ramos superantibus; ramis divergentibus, ca. 10-floris. Bracteae florigerae late obovatae vel suborbiculares, 1 cm longae, apice apiculatae cucullataeque, rubrae (Steyermark), tenues; floribus sessilibus, divergentibus. Sepala 17 mm longa, ad 3 mm connata lobis liberis ellipticis, obtusis, forte nervatis; petalis luteis (Steyermark), laminis ellipticis, 7 mm longis; staminibus inclusis; antheris 4 mm longis.

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ADICIONES A LAS LEGUMINOSAS DE LA FLORA DE NICARAGUA[1]

MARIO SOUSA S.[2]

RESUMEN

Se describen nueve especies nuevas para la ciencia y se hace una nueva combinación en la familia Leguminosae para la *Flora de Nicaragua*. De estas una corresponde a las Mimosoideae (**Pithecellobium campylacanthus**) y las otras a las Papilionoideae, de ellas cinco son Millettieae (**Lonchocarpus ferrugineus, L. monticolus, L. morenoi, L. pilosus** y **L. verrucosus**) y tres Robinieae (**Coursetia apantensis, C. elliptica,** y **C. paucifoliolata**). La nueva combinación es en el género *Lonchocarpus* (**L. acuminatus**) de una especie hasta ahora mal entendida, pero de amplia distribución.

ABSTRACT

Nine new species are described and one new combination is made in the family Leguminosae for the *Flora de Nicaragua*. One of the new species belongs to the subfamily Mimosoideae (**Pithecellobium campylacanthus**) and the others to the Papilionoideae, of which five belong to the tribe Millettieae (**Lonchocarpus ferrugineus, L. monticolus, L. morenoi, L. pilosus,** and **L. verrucosus**) and three to the Robineae (**Coursetia apantensis, C. elliptica,** and **C. paucifoliolata**). The single new combination is made in the genus *Lonchocarpus* (**L. acuminatus**) and represents a poorly understood but widespread species.

De los grupos de leguminosas que se nos invitó a participar para el proyecto *Flora de Nicaragua*, hasta la fecha han resultado novedades, particularmente en *Lonchocarpus, Coursetia,* y *Pithecellobium*; en *Lonchocarpus,* un género que en Nicaragua está representado al menos por 21 especies, cuenta con tres endémicas para el país, en este género el problema es contar con material completo, es decir, flores, frutos y de preferencia plántulas, lo cual, en general no es posible, ya que su diversidad es grande y entre más caracteres se cuente, su ententimiento y relaciones son más claras. Es de notar que las especies de selva alta perennifolia de la vertiente Caribe están poco representadas en los herbarios, por lo que, es aquí donde en un futuro deben aparecer nuevos registros. El género *Coursetia* es muy interesante en Nicaragua, de las tres especies disponibles, las tres son nuevas para la ciencia, dos endémicas y otra compartida con Costa Rica, las tres pertenecen al mismo grupo: *Madrensis* Rydberg. De la especie nueva de *Pithecellobium,* en Nicaragua se encuentra su límite sur y en México en el Itsmo de Tehuantepec, es donde mejor se le conoce.

MIMOSOIDEAE

Pithecellobium campylacanthus L. Rico & M. Sousa, sp. nov. TIPO: 7 km al O-NO de Tehuantepec, distrito de Tehuantepec, Oaxaca, México, 17 marzo de 1981, *M. Sousa 11938* (holotipo, MEXU; isotipos, BM, MO). Figure 1.

Frutices vel arbores usque ad 14 m; caulis ramique spinis stipularibus curvis, persistentibus armati; lenticellis numerosis albidis praediti. Folia 5.5–11 cm longa; petiolus prope basem glandula singulari instructus; rhachis (2.2–)3.5–5 cm longa, villosa vel pilosa, (6–)9–13 paribus pinnarum praedita, quaque pinna 2.5–4 cm longa, in paribus ultimis 1–2 glandulis instructa; foliola in (11–)18–26 pares per pinnam disposita, 2.5–6(–7) mm longa, (1–)1.5–2 mm lata, lineari-oblonga, villosa vel glabrescentia, ventraliter nitida, dorsaliter obscurioria, base oblique truncata, apice acuta. Inflorescentia fasciculos e 2 capitulis compositos formans, pedunculis 2.3–4 cm longis, villosis; capitula 2.5–3 cm diametro sub florescentia, bractea florali 1.5 mm longa; flores albi; calyx carollaque 5-lobulatae, in lobulis strigulosae; tubus staminialis in corolla insertus; ovarium sessile glabrumque. Legumen secus ambas suturas dehiscens, 11.2–16 cm longum, 1.8–2.6 cm latum, 1–6.4 mm crassum, stipite usque ad 2 cm longo, apice api-

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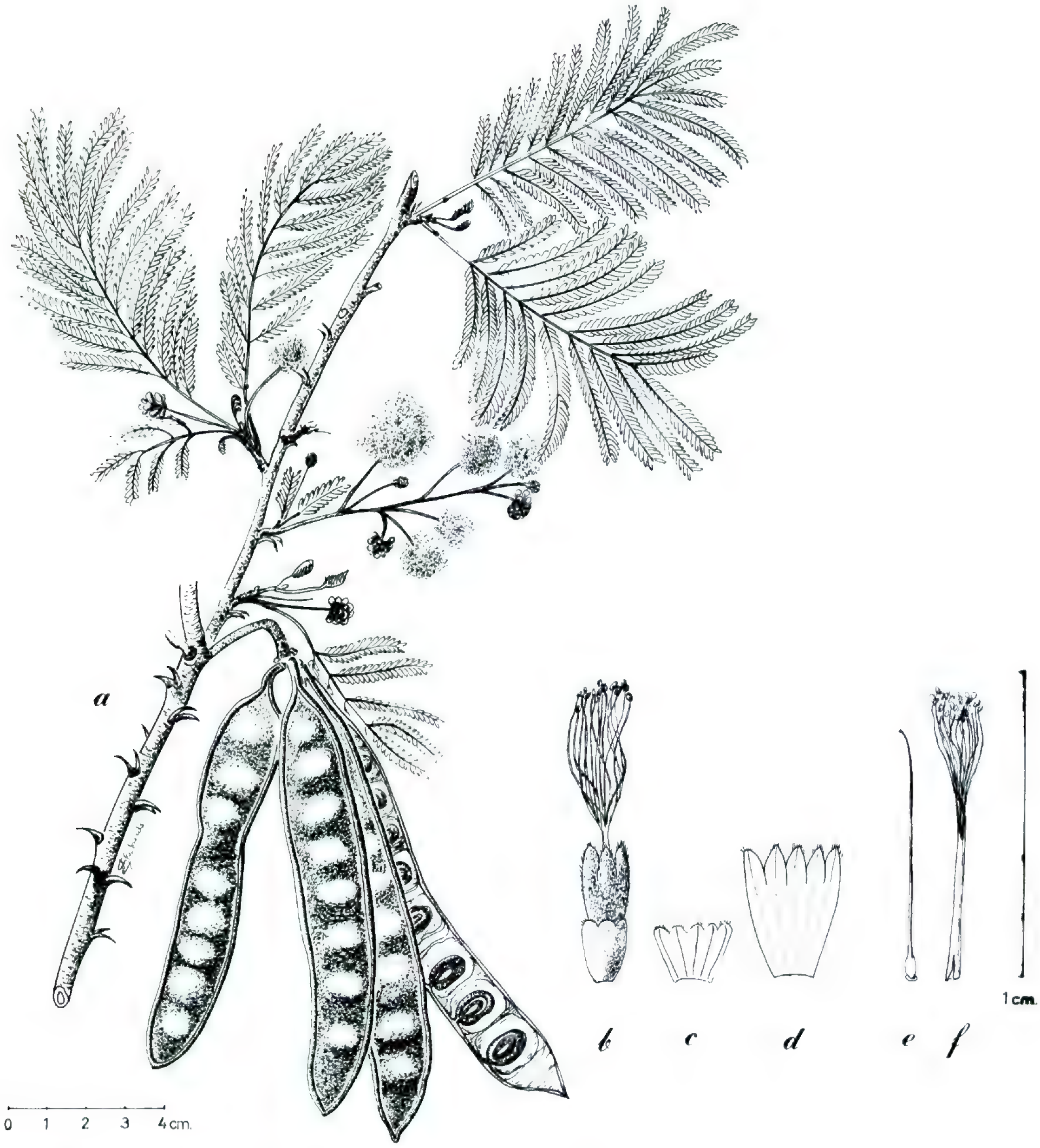

FIGURE 1. *Pithecellobium campylacanthus.*—a. Rama con inflorescencias y frutos.—b. Flor completa.—c. Cáliz.—d. Corola.—e. Gineceo.—f. Androceo. Tomado de *Sousa 11938.*

culatum. Semina late ellipsoidea, 1.3–1.4 cm longa, 0.9–1.0 cm lata, 3 mm crassa.

"Uña de gato", "Guamuchil" (Oaxaca, México).

Arbustos o árboles, hasta de 14 m de alto; tallos y ramas armados con espinas estipulares curvas, persistentes; ramas con numerosas lenticelas blanquecinas. Hojas 5.5–11 cm de largo; pecíolo 2.5–3 cm de largo, de viloso a piloso con la edad, con una glándula cercana a la base o por debajo de la mitad de éste; raquis (2.2–)3.5–5 cm de largo, de viloso a piloso, con (6–)9–13 pares de pinnas, 2.5–4 cm de largo, con 1 o 2 glándulas entre los últimos pares de pinnas; folíolos de (11–)18–26 pares pon pinna, 2.5–6(–7) mm de largo, (1–)1.5–2 mm de ancho, linear oblongos de vilosos a glabrescentes, más densamente en el envés, brillantes y más oscuros en el haz que en el envés, base oblicuamente truncada, ápice agudo, venación reticulada, marcada en ambas superficies. Fascículos de 2 capítulos, pedúnculos

2.5–4 cm de largo, vilosos; capítulos 2.5–3 cm de diámetro en las antesis; bráctea floral de 1.5 cm de largo, claviforme, pubescente en el ápice. Flores blancas; cáliz 5-lobulado, estriguloso en los lóbulos; corola el doble del tamaño del cáliz, 5-lobulada en un cuarto de su largo, estrigulosa en los lóbulos, tubo estaminal inserto en la corola; ovario sésil y glabro. Legumbre dehiscente, 11.2–16.5 cm de largo, 1.8–2.6 cm de ancho, 1–6.4 mm de grueso, plana, recta, los márgenes evidentes cuando inmadura, las valvas coriáceas, de hírtulas a glabras, base aguda y con un estípite hasta de 2 cm de largo, ápice apiculado a veces rostrado, el rostro llega a medir hasta 8 mm de largo; semillas anchamente elipsoides, 1.3–1.4 cm de largo, 0.9–1 cm de ancho y 3 mm de grueso, pardo oscuras, la línea fisural un poco más clara.

Distribución. En México en la costa del Pacífico en los estados de Guerrero y Oaxaca, abundante en el área del Istmo de Tehuantepec, en Centro América en Honduras y Nicaragua. En selva baja caducifolia, es frecuente como riparia en arroyos de temporal. Altitudes desde el nivel del mar hasta 200 m en México, y de 120 a 700 m en Centro América. Florece de febrero a mayo e inicia su fructificación en mayo, pudiéndose encontrar frutos en diferentes estados de maduración durante todo el año.

MEXICO. GUERRERO: Zihuatanejo, Col. Vicente Guerrero, *M. T. Germán 351* (MEXU). OAXACA: Distr. de Tehuantepec, Presa Benito Juárez, *E. S. Blanco 25* (MEXU); El Salado, a 13 km al NO de Jalapa del Marqués, *R. Cedillo T. 1079* (MEXU); 14 km al O de Salina Cruz, *F. González Medrano 11989* (MEXU); Tequisistlán, *R. Hernández M. 91, 122b* (MEXU); 10 a 15 km al NO de Tehuantepec, *R. M. King 752* (MEXU); 3 millas al SO de Tehuantepec, *E. Lathrop 5944* (MEXU); 3 km al N de la carr. en el camino a la Presa Benito Juárez, *A. S. Magallanes 215* (MEXU); Tehuantepec, *E. Matuda 28566, 28567* (MEXU); a 21 km al O de Tehuantepec, *M. Sousa 5026* (MEXU); Crucero Sta. Elena, desv. a Cozoaltepec, a 26 km al E-SE de Pto. Escondido, *Sousa 6427* (MEXU); a 3 km al E de Marilú, a 17 km al NE de La Reforma, carr. Oaxaca-Tehuantepec, *Sousa 6578* (MEXU); a 22 km al SO de Salina Cruz, *Sousa 7455* (MEXU); a 11 km al O-NO de Tehuantepec, *Sousa 7472* (MEXU); a 1 km a N de Playa Chipehua, *Sousa 8663* (MEXU); a 27 km al SO del Morro, al E de San Pedro Huamelula, *Sousa 8674* (MEXU); desv. a Playa Chipehua, carr. Salina Cruz-Pochutla, *Sousa 9138, 9139* (MEXU); a 8 km al NO de Tehuantepec, *Sousa 10093* (MEXU); desv. a Playa Chipehua, a 8 km al SO del Morro de Mazatán, *Sousa 10134* (MEXU); a 13 km al NO de Santiago Laollaga, *Sousa 10181* (MEXU); a 17 km al N-NO de Tehuantepec, *Sousa 11944* (MEXU); a 1 km al SO de San Pedro Huilotepec, *O. Téllez 154* (MEXU); a 3 km al NE de Santiago Laolloga, *Téllez 231* (MEXU); a 9 km al NE de Tehuantepec, *Téllez 247* (MEXU); Paso Alicia, 8 km al N-NO de Tehuantepec, *R. Torres 502* (MEXU); a 7 km al NO de Tehuantepec, *Torres 688* (MEXU); Rancho Lizet, 3.5 km al SO de la entrada a Buenos Aires, *Torres 4789* (MEXU). Distr. de Juchitán: a 4 km al N de Matías Romero, *R. M. King 683* (MEXU); a 3 km al NE de Juchitán, *M. Sousa 6596* (MEXU); Ixtepec, *Sousa 8720* (MEXU); La Venta, *Sousa 9566* (MEXU); a 6 km al N de La Ventosa, *Sousa 9608* (MEXU).

HONDURAS. COMAYAHUA: El Banco, *J. V. Rodríguez 2439* (GH); Río Selguapa, *Rodríguez 2560* (GH); Valle entre Comayahua y San Antonio de las Flores, *L. O. Williams & A. Molina 12602* (GH, MEXU).

NICARAGUA. BOACO: Mpio. de Teustepe, km 60 carr. al Rama, *P. P. Moreno 3748* (MEXU, MO); Hacienda El Sitio, km 61 carr. al Rama (No. 7), Quebrada San Bartolo, *Moreno 10041* (MEXU, MO).

Pithecellobium campylacanthus pertenece a la Sección *Ortholobium* Benth., la que se caracteriza por tener estípulas espinescentes, varios pares de pinnas y folíolos, frutos planos y semillas sin arilo. Especies afines a él son: *P. sonorae* y *P. leptophyllum* los que tienen menor número de pinnas, las flores y los frutos son más pequeños y el habitat es matorral xerófilo; de *P. elachistophyllum* difiere principalmente en la forma de los folíolos y el fruto curvo. El nombre de esta especie hace referencia a que sus espinas estipulares son curvas.

Es una especie que en el área del Istmo de Tehuantepec sus poblaciones son muy variables tanto en la coloración de los folíolos, desde concoloros hasta discoloros brillantes, como en la pelosidad, desde vilosa a glabrescente; se ha tratado de ver si hay una correlación de estos caracteres tan variables con respecto a la época del año, siendo que es una especie que se localiza en selva baja caducifolia donde hay una marcada estacionalidad de lluvias, o de acuerdo a la distribución altitudinal, pero parece ser que esta variación es independiente a dichos factores.

PAPILIONOIDEAE

MILLETTIEAE

Lonchocarpus acuminatus (Schldl.) M. Sousa, comb. nov. *Robinia acuminata* Schlechtendal, Linnaea 12: 306, 307. 1838. TIPO: México. Veracruz: *C. J. W. Schiede* (holotipo, B, destruido; lectotipo aquí designado, HAL, foto MEXU!).

Lonchocarpus purpusii Brandegee, Univ. Calif. Publ. Bot. 6: 500. 1919. Hermann, J. Wash. Acad. Sci. 38: 13. 1948. TIPO: México, Veracruz: *C. A. Purpus 7849* (holotipo, UC!; isotipos, A!, GH!, MO!, US!).

Lonchocarpus chiapensis Lundell, Wrightia 1: 152, 153. 1946. Hermann, J. Wash. Acad. Sci. 38: 310. 1948. TIPO: México. Chiapas: *E. Matuda 5008* (holotipo, LL; isotipos, MEXU!, MO!).

Lonchocarpus nicaraguensis Lundell, Wrightia 1: 154. 1946. Hermann, J. Wash. Acad. Sci. 38: 311. 1948. TIPO: Nicaragua. Managua: *S. S. White & C. L. Gilly* (holotipo, LL; isotipo, ENCB!).

Esta especie ha sido confundida con *L. peninsularis* (J. D. Smith) Pittier (ver Hermann, 1965), *L. nicoyensis* (J. D. Smith) Pittier (ver Hermann, 1965), *L. cochleatus* Pittier (ver Hermann, 1965), y *L. kerberi* Harms (ver Hermann, 1948). *Lonchocarpus acuminatus* difiere de *L. peninsularis* y su sinónimo *L. nicoyensis,* en que en esta última el fruto es subleñoso. De *L. cochleatus,* además de tener *L. cochleatus* un fruto leñoso y más ancho, sus pedúnculos y pedicelos florales son más largos, así como sus plántulas llevan eófilos trifoliolados en vez de unifoliolados. En el caso de *L. kerberi,* es más problemático, ya que, sólo he visto fragmentos (en F), los cuales muestran afinidades con *L. caudatus* Pittier. *Lonchocarpus acuminatus* se trata de una especie de amplia distribución, de Veracruz a Panamá, en bajas altitudes y en climas cálidos secos.

Lonchocarpus ferrugineus M. Sousa, sp. nov. TIPO: Costa Rica. Heredia: A lo largo de un arroyo, como a 5 km al N de San Miguel, 20 enero de 1971, *G. S. Hartshorn 985* (holotipo, MEXU; isotipo, CR). Ilustración: Holdridge y Poveda A. (1975), determinado como *Lonchocarpus velutinus* Benth.

Arbores; cortex interior ubi incisus succum resinaceum emittens; rami juniores fistulosi, angulati, ferrugineo-tomentosi; petiolus 8–14 cm longus, profunde canaliculatus; rhachis foliaris tomentosa, ut in petiolo canaliculata; folia 7–9-foliolata, foliolis epunctatis, vulgo ellipticis vel oblongis, (7–)11–17(–22) cm longis, 5–7.5(–11) cm latis, ventraliter rugosis, dorsaliter nervis prominentibus instructis. Inflorescentiae (tantum in tempore fructificati visae) (9–)15–22 cm longae; bractea peduncularis ensiformis, 2–2.5 mm longa; pedunculi florales usque ad 1.5 mm longi; pedicelli 2–3 mm longi. Legumen indehiscente, coriaceum, ellipticum vel lanceolatum, planum, lateraliter compressum, 11–20 cm longum, 2.5–4 cm latum, dense ferrugineo-velutinum vel tomentosum; semina 1–3 per fructum; sutura vexillaris anguste alata, carinalis carinata.

"Zopilote" (Nicaragua); "Comenegro" (Costa Rica).

Arboles de 8–25 m de alto; la corteza interior con fluido resinoso al corte; ramas jóvenes fistulosas, anguladas, densamente ferrugíneo tomentosas, lentícelas poco visibles por el tomento. Hojas estipuladas, estípulas pronto deciduas, no vistas; pecíolo 8–14 cm de largo, profundamente canaliculado, ferrugíneo tomentoso; raquis foliar tomentoso y canaliculado como el pecíolo, 8–13 cm de largo; hojas 7–9-folioladas, la terminal en ocasiones más grande que las laterales; folíolos cartáceos, epunteados, elípticos a oblongos, en ocasiones ovados a obovados, (7–)11–17(–22) cm de largo, 5–7.5(–11) cm de ancho, base cuneada a redondeada, ápice agudo a corto acuminado, en el haz rugosos y densamente ferrugíneo tomentosos sobre las venas media y secundarias, o esparcidamente tomentosas, en el envés las nervaduras de primero a tercer orden marcadamente realzadas, tomentosos en las nervaduras y velutinos en las áreas intervenosas, nervaduras secundarias 9–14. Inflorescencias (sólo fueron vistas en fruto) pedunculadas, (9–)15–22 cm de largo; bráctea peduncular ensiforme, 2–2.5 mm de largo; pedúnculos florales hasta 1.5 mm de largo; pedicelos 2–3 mm de largo. Legumbre indehiscente, coriácea, elíptica a lanceolada, largo atenuada en la base, atenuada a redondeada en el ápice, plana, lateralmente compresa, 1–3 semillas por fruto, ligeramente constricta entre las semillas sobre las suturas, 11–20 cm de largo, 2.5–4 cm de ancho, densamente ferrugíneo velutina a tomentosa, sutura vexilar angostamente alada, sutura carinal angostamente aquillada; semillas maduras no fueron vistas.

Distribución. De Nicaragua a Panamá, en climas muy húmedos, en altitudes de 450 a 625 m. Fructifica de septiembre a abril.

NICARAGUA. ZELAYA: Mpio. de Nueva Guinea, Bocas de Piedra, *A. Laguna 135* (MO).

COSTA RICA. HEREDIA: San Miguel de Sarapiqui, *L. R. Holdridge 5129* (F). CARTAGO: Instituto Turrialba, *J. León 2264* (CR, F); Puente Cajón, Turrialba, *L. J. Poveda 26* (CR).

PANAMA. ZONA DEL CANAL: Isla de Barro Colorado, Van Tyne 13, *R. Foster 2901* (F).

Sus relaciones no son muy claras por carecerse de la información de material en flor, sin embargo, por sus largas brácteas florales, fruto cuya sutura vexilar es alada, además de la venación de los folíolos y tipo de pelosidad, la especie más afin parece ser *L. orizabensis* Lundell, de la cual difiere por tener menos folíolos por hoja, pecíolo y raquis profundamente canaliculados y frutos más grandes. Su nombre específico aduce al color de tallos jóvenes, pecíolos, envés de las hojas, inflorescencias y frutos.

Lonchocarpus monticolus M. Sousa, sp. nov. TIPO: Nicaragua. Dept. Estelí: Cerro Tisey, a 8 km al SE de Estelí, 5 noviembre de 1981, *O. Téllez 4842 con P. P. Moreno* (holotipo, MEXU; isotipos, BM, MO).

Frutices vel arbusculae, foliis 5-foliolatis, foliolis pellucido-punctatis, ellipticis, ovatis vel obovatis, (1.5–)2.5–5(–7.5) cm longis, (1–)2–3(–3.5) cm latis, ventraliter sparsim sericeis demum glabris. Inflorescentiae laxae, 2–3 cm longae; florescentia coaetanea; pedunculi florales 4–6 mm longi, pedicellis 2–3 mm longis, bracteolis in apice pedicelli oppositis, parvis, oblongis; flos 10 mm longus; calyx glandularis pellucido-punctatus, 3 mm longus, 6 mm latus, sparsium canescenti-sericeus, paene truncatus; corolla inter nervos petalorum lineis punctisque glandularibus, translucidis, abundis vestita; vexillum praeter regionem in base superficies externae paene glabrum. Legumen indehiscente, subcoriaceum, ellipticum vel lanceolatum, planum, 1–3 seminibus per fructum gaudens, constrictum supra suturas inter semina, 4–10.5 cm longum, 1.8–2.2 cm latum, glabrum, suturis anguste carinatis.

Arbustos a arbolitos, hasta 5 m de alto; la corteza interior sin fluido resinoso al corte; ramas esparcidamente seríceas, pronto glabras, con lenticelas orbiculares a elípticas, cremas. Hojas estipuladas, estípulas pronto deciduas, orbiculares a anchamente ovadas, 0.8–1 mm de largo, 0.9–1.1 mm de ancho; pecíolo (0.7–)1.5–2.5 cm de largo; raquis foliar seríceo como las ramas, 2.5–4 cm de largo, hojas 5-folioladas, la terminal más grande que las laterales; folíolos cartáceos, pelúcido punteados, elípticos, ovados a obovados, (1.5–)2.5–5(–7.5) cm de largo, (1–)2–3(–3.5) cm de ancho, base cuneada a redondeada, ápice obtuso a acuminado, opacos y esparcidamente canescente seríceos a pronto glabros en el haz, en el envés seríceos a glabrescentes, nervadura primaria y secundarias realzadas en el envés, nervaduras secundarias 4–6. Inflorescencias corto pedunculadas, laxas, 2–3 cm de largo; floración coetánea; pedúnculos florales 4–6 mm de largo, pedicelos 2–3 mm de largo, bracteolas opuestas, en el ápice del pedicelo, oblongas, 0.7–0.9 mm de largo. Flores 10 mm de largo; cáliz ciatiforme, glandular pelúcido punteado, 3 mm de largo, 6 mm de ancho, esparcidamente canescente seríceo, más densamente en el margen, casi trunco; corola azul (*Moreno 8728*) [probablemente púrpura], con abundantes líneas y puntos glandulares translúcidos entre las nervaduras de los pétalos, todos los pétalos canescente seríceos; estandarte reflexo, su lámina cóncava, orbicular, 10 mm de ancho, casi glabra excepto en la base de la superficie externa; anteras glabras; ovario seríceo, 6-ovulado. Legumbre indehiscente, subcoriácea, elíptica a lanceolada, plana, atenuada en la base, ápice rostrado, lateralmente compresa, 1–3 semillas por fruto, constricta entre las semillas sobre las suturas, 4–10.5 cm de largo, 1.8–2.2 cm de ancho, glabras, suturas angostamente aquilladas; semillas 13 mm de largo, 8 mm de ancho, 3.5 mm de grueso, morenas.

Distribución. Conocida solamente en el sur del departamento de Estelí en Nicaragua, en altitudes entre 1,200 y 1,300 m. Habita en bosque de pino-encino. Florece en mayo y fructifica de fines de septiembre a noviembre.

NICARAGUA. ESTELÍ: San José de La Laguna, *P. P. Moreno 8096* (MO); a 8 km de la Carretera Panamericana, camino a San Nicolás, 12°59′N, 85°21′O, *Moreno 8728 & J. Henrich* (MEXU, MO); 1.5 km al N del Valle de San José de La Laguna, camino a San Nicolás, 12°58′N, 86°21′O, *Moreno 11353* (MO); faldas del Cerro Tisey, 12°58′N, 85°22′O, *Moreno 12737* (MO); San José, 10 km SE de Estelí, *O. Téllez 4800 con Moreno* (MEXU).

Esta especie quedaría en la Serie 2. *Planinervi,* Sección 1. *Punctati* de Pittier, cercana a *L. acuminatus,* del cual difiere: por el ápice obtuso de sus folíolos; sus inflorescencias más cortas; pedúnculos florales más largos; fruto sin ala en la sutura vexillar y por tratarse de una especie más mesófila. El nombre específico fué dado por su hábitat montícola.

Lonchocarpus morenoi M. Sousa, sp. nov. TIPO: Nicaragua. Dept. Estelí: Cerro Quiniento, Hda. La Grecia, Mpio. San Juan de Limay, 2 septiembre de 1980, *P. P. Moreno 2155* (holotipo, MEXU; isotipo MO). Figure 2.

Frutices vel arbusculae, foliis 5–7-foliolatis, foliolis epunctatis, ellipticis, interdum ovatis vel obovatis, (2–)4–6.5(–8.5) cm longis, (1.4–)2.2–3.5 cm latis, ventraliter opacis glabrisque. Inflorescentiae pedunculatae, 4–11 cm longae; florescentia coaetanea; pedunculi florales e minus quam 1 mm longi, pedicellis 2–3 mm longis, bracteolis oppositis, parvis, in ⅓ distali pedicelli, oblongis vel ellipticis; flos 11–12 mm longus; calyx 3 mm longus, 6 mm latus, canescenti-sericeus, paene truncatus; corolla purpurea. Legumen indehiscente, subligneum, anguste ellipticum vel lanceolatum, longostipitatum, apice rostratum, lateraliter compressum, 1–2 seminibus per fructum gaudens, profunde inter semina constrictum, 8–11 cm longum, 2–2.4 cm latum, glabrum vel subglabrum, sutura vexillari 8–9.5 mm crassa, concava, costa media infirme effecta.

Arbustos a árboles de 2–5 m de alto; la corteza sin fluido resinoso al corte; ramas esparcidamente seríceas cuando jóvenes, posteriormente glabras, con lenticelas orbiculares a elípticas, cre-

FIGURE 2. *Lonchocarpus morenoi.*—a. Rama con inflorescencias.—b. Estípula.—c. Botones florales, mostrándose las bracteolas.—d. Frutos, uno enseña el márgen vexilar.—e. Cáliz con pedúnculo y pedicelo.—f. Estandarte.—g. Ala.—h. Quilla.—i. Tubo estaminal.—j. Gineceo. Las hojas y flores fueron tomadas de *Moreno 8356* y los frutos de *Moreno 2155*.

mas. Hojas estipuladas, estípulas pronto deciduas, elípticas a anchamente ovadas, 0.6–1 mm de largo, 0.6–1.1 mm de ancho; pecíolo 2.3–3.5 cm de largo; raquis foliar seríceo como las ramas, 2.5–4 cm de largo; hojas 5–7-folioladas, la terminal más grande que las laterales; folíolos cartáceos o coriáceos, epunteados, elípticos, algunas veces ovados u obovados, (2–)4–6.5(–8.5) cm de largo, (1.4–)2.2–3.5 cm de ancho, base cuneada, ápice obtuso, en ocasiones corto acuminado, opacos y glabros en el haz, en el envés canescente seríceos en las nervaduras y velutinos y seríceos en las áreas internervaduras, nervadura primaria y secundarias realzadas en el envés, nervaduras secundarias de 6–8. Inflorescencias pedunculadas, 4–11 cm de largo, flores esparcidas, en el tercio superior; floración coetánea; pedúnculos florales de menos de 1 mm de largo; pedicelos 2–3 mm de largo; bracteolas opuestas, en el tercio superior del pedicelo, oblongas a elípticas, 1–1.2 mm de largo. Flores 11–12 mm de largo; cáliz ciatiforme, epunteado, 3 mm de largo, 6 mm de ancho, canescente seríceo, casi trunco, sólo presentes los tres dientes carinales, el medio 0.2 mm de largo; corola morada (*Moreno 8356*), epunteada, todos los pétalos canescente seríceos; estandarte reflexo, su lámina profundamente cóncava, transversalmente ancho elíptica, 10–11 mm de ancho, moderadamente pelosa en la superficie externa; anteras glabras; ovario canescente seríceo, 5-ovulado. Legumbre indehiscente, subleñosa, angosto elíptica a lanceolada, largo estipitada, largo atenuada hacia el ápice rostrado, lateralmente compresa, 1 o 2 semillas por fruto, profundamente constricta entre las semillas sobre las suturas y lateralmente, 8–11 cm de largo, 2–2.4 cm de ancho, glabra o casi, sutura vexilar 8–9.5 mm de gruesa, cóncava, con una costilla media poco desarrollada, sutura carinal angostamente aquillada; semillas maduras no fueron vistas.

Distribución. Unicamente conocida de Nicaragua, en el departamento de Estelí, en altitudes entre 500 y 870 m. Florece en abril y fructifica en septiembre.

NICARAGUA. ESTELÍ: Valle Canarias, entre San Juan de Limay y Pueblo Nuevo, Mpio. San Juan de Limay, *P. P. Moreno 2413* (MEXU, MO); Escuela de Agricultura, 2 km sobre la carretera a La Laguna de Miraflores, "Llano el Duaque", *Moreno 8356* (MEXU, MO).

Esta especie es cercana a *L. constrictus* Pittier, de la que difiere fundamentalmente por su fruto, que es más ancho y grueso y su sutura vexilar cuenta con una costilla media. Está dedicada a Pedro Pablo Moreno Castillo (1953–), oriundo de Estelí, Nicaragua, prolífico colector (26,000 números) de la Flora de Nicaragua.

Lonchocarpus pilosus M. Sousa, sp. nov. TIPO: Nicaragua. Dept. Matagalpa: Santa María de Ostuma, 20 julio de 1975, *H. B. L. Evans s.n.* (holotipo, MEXU; isotipo, FHO). Figure 3.

Arbores; rami juvenales ferrugineo-pilosi. Folia 9–11-foliolata, stipulata, stipulis deciduis, erectis, lanceolatis, 13–15 mm longis, 2–3 mm latis; petiolus et rhachis pilosa, pilositate simili ramorum; foliola epunctata, margine revoluta, elliptica, oblonga vel obovata, 3.5–8 cm longa, (1–)1.5–2.7(–3.2) cm lata, supra et subtus laxe pilosa, nervatione craspedodroma prominenti; nervi secundarii 15–25. Legumen indehiscens, coriaceum vel leviter suberosum, ellipticum, ad basem et apicem attenuatum, planum, compressum, 1–3-seminalis, 8.5–12(–21) cm longum, 4–5 cm latum, dense ferrugineo-velutinum, suturis anguste carinatis.

Arboles de 4–25 m de alto, probablemente perennifolios; la corteza interior sin fluido resinoso al corte; ramas jóvenes laxamente ferrugíneo pilosas, pronto glabras, con lenticelas orbiculares, cremas. Hojas estipuladas, estípulas deciduas, erectas, lanceoladas, 13–15 mm de largo, 2–3 mm de ancho; pecíolo 3–5.5 cm de largo; raquis foliar piloso como las ramas, 5–8 cm de largo, hojas 9–11-folioladas, la terminal ligeramente más grande que las laterales; folíolos cartáceos, epunteados, 3.5–8 cm de largo, (1–)1.5–2.7(–3.2) cm de ancho, elípticos, oblongos a ligeramente obovados, con los márgenes generalmente revolutos, base cuneada, en ocasiones redondeada, ápice obtuso a redondeado, emarginado, a mucronado, mucrón hasta 3 mm de largo, opacos y laxamente pilosos pronto glabros en el haz, en el envés pilosos particularmente sobre las nervaduras, nervación craspedódroma, nervadura primaria y secundarias realzadas en el envés, nervaduras secundarias de 15–25. Inflorescencias (sólo fueron vistas en fruto) pedunculadas, 5.5–10 cm de largo; pedúnculos florales 3–5 mm de largo, pedicelos 4–6 mm de largo. Legumbre indehiscente, coriácea a ligeramente suberosa, elíptica, atenuada en la base y en el ápice, plana, lateralmente compresa, 1(–3) semillas por fruto, 8.5–12(–21) cm de largo, 4–5 cm de ancho, densamente ferrugíneo velutina, suturas angostamente aquilladas; semillas 16.5 mm de largo, 10 mm de ancho, 4 mm de grueso, moreno-rojizo oscuras.

FIGURE 3. *Lonchocarpus pilosus.*—a. Rama con infrutescencia.—b. Detalle nervación.—c. Fruto. La infrutescencia y detalle de la nervación tomada de *H. B. L. Evans s.n.* y el fruto de *W. D. Stevens 23155.*

Distribución. Sólo de Nicaragua en Matagalpa y Chontales, en bosque premontano muy húmedo, en ocasiones ripario, entre los 350 y 1,200 m de altitud. Fructifica de mayo a diciembre.

NICARAGUA. MATAGALPA: Matagalpa 12°56′–57′N, 85°55′–56′O, *M. Araquistain 3652* (MEXU, MO); Río Yasica, 20 km al E de Matagalpa, *D. Neill 1983* (HNMN); 1.5 km N de Matagalpa, ca. 12°57′N, 85°55′O, *Stevens 22527* (MEXU, MO). CHONTALES: orilla de Cuapa, 12°16′N, 85°23′O, *Stevens 23155* (MEXU, MO).

Lonchocarpus pilosus está emparentado tanto con *L. phlebophyllus* como con *L. eriocarinalis,* todas ellas poseen nervaduras laterales que se

resuelven en el margen foliolar, pero difiere de ellas por su distintiva pelosidad pilosa, enormes estípulas, y fruto de gran tamaño, además de vivir en hábitats húmedos de montaña y no en selvas caducifolias. El nombre específico se refiere a la pelosidad de sus partes vegetativas.

Lonchocarpus verrucosus M. Sousa, sp. nov. TIPO: Mexico, Chiapas: Vega del Río Naranjo, entre Santa Rita y El Real, E de Ocosingo, Mpio. Ocosingo, 8 marzo de 1951, *F. Miranda 7135* (holotipo, MEXU; isotipo, US). Figure 4.

Arbores altae, sempervirentes; ramunculi lenticellas numerosas gerentes quae accrescentes coalitaeque demum producentes pagina verrucosa. Folia stipulata, stipulis deciduis, erectis, anguste ovatis vel subulatis, elongatis angustatisque; petiolis brevibus; foliis 9–11-foliolatis; foliolis magnis, 6–11 cm longis, 3.5–6.5 cm latis, epunctatis, elliptico-oblongis, apice obtusis vel retusis, base rotundatis, plus minusve bicoloratis. Inflorescentia pedunculata; florescentia coaetanea; pedunculis floralibus 2–3 mm longis; pedicellis 3–4 mm longis; bracteolis plus minusve alternatis, calyce distantibus, filiformibus, parvisi. Flor 6–7 mm longus; calyce cyathiformi, paene truncato, tantum tres dentes anteriores gerente; corolla epunctata; vexillo erecto cum lamina concavo; antheris glabris. Fructus indehiscens, coriaceus, ellipticus vel oblongus, apice rotundatus rostratusque, basi attenuatus, pauciseminalis, medio magnitudine, suturo vexillari interdum parum alato; seminibus reniformibus, rubellobrunneis. Cotyledones epigeae; eophylla opposita, unifoliolata.

"Shi-inte", "Gusano colorado" (Chiapas, México).

Arboles hasta 20 m de alto, perennifolios; la corteza interior sin fluido resinoso al corte; ramas laxamente canescente velutinas, pronto glabras; las lenticelas de elípticas a linear oblongas, agrandándose y algunas veces fusionándose con la edad dando una superficie verrucosa. Hojas estipuladas, estípulas pronto deciduas, erectas, angostamente ovadas a subuladas, 6–7 mm de largo, 1–1.5 mm de ancho en la base; pecíolo 6.5–9 cm de largo; raquis foliar glabro, 10–13.5 cm de largo; hojas 9–11-folioladas; folíolos cartáceos, epunteados, elíptico oblongos, algunas veces ovados, 6–11 cm de largo, 3.5–6.5 cm de ancho, base ligeramente cuneada, ápice de obtuso a retuso, ligeramente bicoloros, verdosos y glabros en el haz y blanquecinos y moderadamente canescente seríceos en el envés, nervaduras laterales 9–12. Inflorescencias pedunculadas, 11–15 cm de largo; floración coetánea; pedúnculos florales 2–3 mm de largo; pedicelos 3–4 mm de largo; bracteolas subopuestas a alternas, de la mitad al tercio superior del pedicelo, filiformes, 1.1–1.2 mm de largo. Flores 6–7 mm de largo; cáliz ciatiforme, epunteado, 2–2.5 mm largo, 4 mm de ancho, esparcidamente a moderadamente canescente seríceo, casi trunco, solo presentes los tres dientes carinales, el medio 0.7 mm de largo; corola roja, epunteada, todos los pétalos canescente seríceos; estandarte erecto, su lámina cóncava, transversalmente ancho elíptica, 7.5 mm de ancho, moderadamente a densamente pelosa en las venaciones de la superficie externa; anteras glabras; ovario seríceo, 6-ovulado. Legumbre indehiscente, coriácea, de elíptica a oblonga, atenuada en la base, redondeada y rostrada en el ápice, lateralmente compresa, 1 o 2 semillas por fruto, 8.5–11 cm de largo, 1.8–2.1 cm de ancho, esparcidamente velutina a glabra, sutura vexillar en ocasiones alada, ala 1 mm de ancho, más comúnmente ambas suturas angostamente aquilladas; semillas 13 mm de largo, 7.5 mm de ancho, 2.5 mm de grueso, moreno-rojizas. Plántulas con cotiledones epígeos; eófilos opuestos, unifoliolados.

Distribución. De Veracruz y Chiapas en México hasta Nicaragua, en selvas altas perennifolias con *Terminalia, Manilkara* y *Swietenia,* frecuente como ripario, en selvas altas y bosques de galería con *Taxodium,* en suelos calizos, del nivel del mar a 1,200 m. Florece en marzo a mayo, fructifica a partir de mayo y aún tiene frutos en enero.

MEXICO. VERACRUZ: a 2 km al N de Uxpanapa, Mpio. Minatitlán, *T. Wendt 4850* (MEXU). CHIAPAS: tributario del Río Jataté, cerca de la Finca El Real, Mpio. Ocosingo, *D. E. Breedlove 15630* (DS); Agua Azul, 60 km S de Palenque, Mpio. Palenque, *Breedlove 49571* (DS, MEXU); San Jerónimo Tulijá, Mpio. de Yajalón, *J. Chavelas P. 3019, G. Alanis & M. Rosas* (MEXU, MICH, US); Emiliano Zapata, *González L. & Hernández P. 323* (MEXU); entre Santa Rita y El Real, E de Ocosingo, *F. Miranda 7137* (MEXU); entre Monte Líbano al Censo, E de Ocosingo, *Miranda 7179* (MEXU); orilla del Río Santo Domingo, a la altura del poblado de Santo Domingo, Mpio. Ocosingo, *M. Sousa 12402, G. Davidse, A. Chater & E. Cabrera* (BM, DS, MEXU, MO).

GUATEMALA. HUEHUETENANGO: 1–2 km ONO de San Antonio Huista, en el camino a Santa Ana Huista, *H. H. Iltis, K. Lind & A. Barrios 138* (F, WIS).

NICARAGUA. ZELAYA: 3.6 km SE Cerro San Isidro, Río Rama, Río Escondido, Bluefields, *G. R. Proctor 27265, G. C. Jones & L. Facey* (F).

Sus relaciones son claras con *Lonchocarpus pentaphyllus,* del cual difiere por contar con mayor número de folíolos, su forma oblonga, bracteolas más chicas y pedúnculos delgados. El

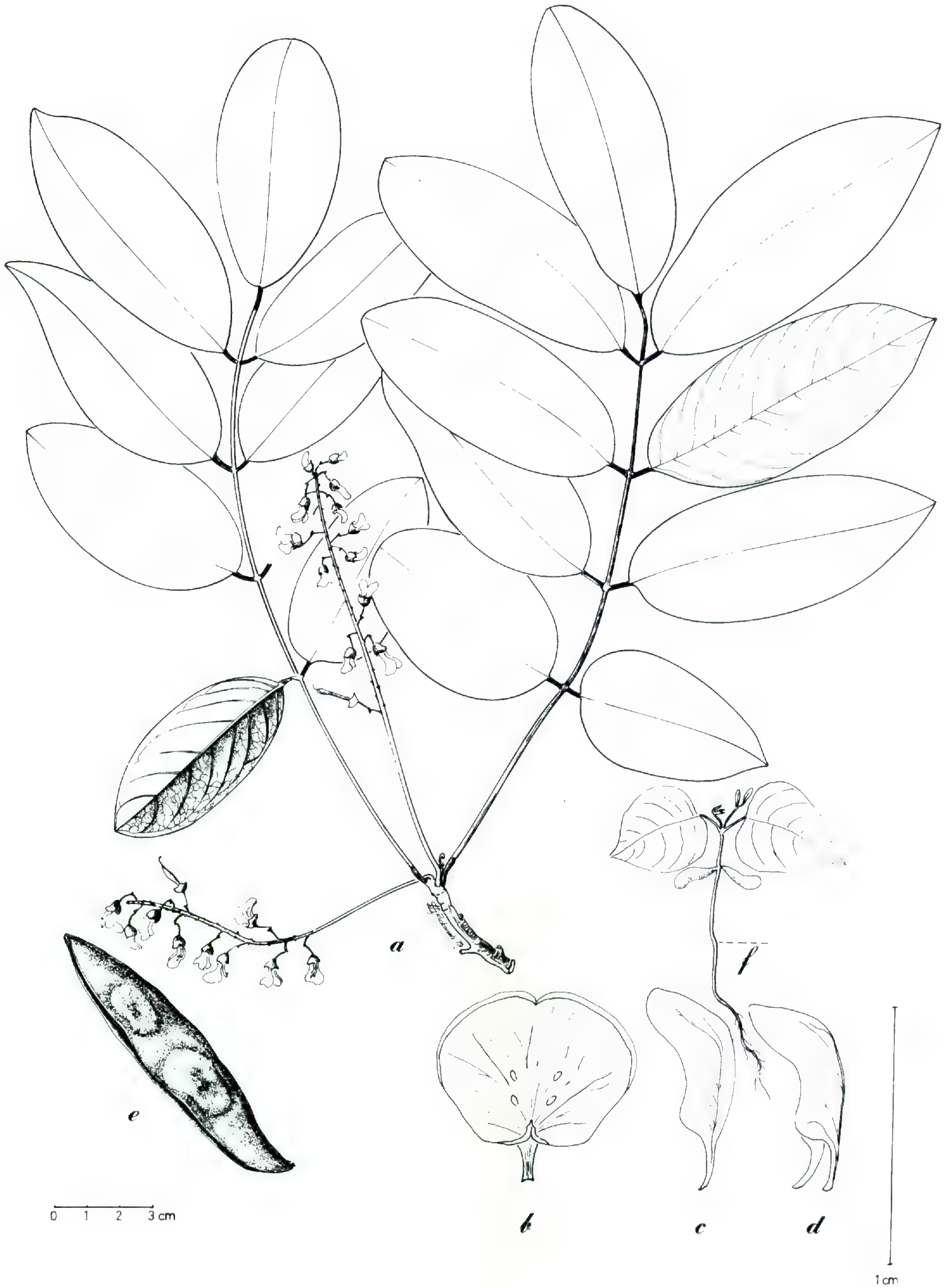

FIGURE 4. *Lonchocarpus verrucosus.*—a. Rama con inflorescencia.—b. Estandartes.—c. Ala.—d. Quilla.—e. Fruto, mostrando el márgen vexilar ligeramente alado.—f. Plántula. Las hojas y flores fueron tomadas de *Miranda 7179,* el fruto de *Chavelas 3019* y la plántula de *Sousa 10402.*

nombre específico se refiere al aspecto de las ramas dado por las lenticelas prominentes.

ROBINIEAE

Coursetia apantensis M. Sousa, sp. nov. TIPO: Nicaragua, Dept. Matagalpa: Cerro Apante, 4 mayo de 1980, *P. P. Moreno 175* (holotipo, MO). Figure 5.

Frutices vel arbusculae, foliis imparipinnatis, (7–)9–15-foliolatis; stipulae persistentes, subulatae vel paene aciculares; rhachis tereticaulis, non alata, canaliculata, velutina, sericea vel subglabra; foliola stipellis persistentibus, acicularibus; pulvinuli 1–1.5 mm longi, dense tomentosi vel subglabri, laminae ellipticae, (1–)2.5–5.5 cm longae, (0.5–)1.5–2.5 cm latae, dorsaliter sparse ventraliterque dense vel sparse sericeae, margine revolubili, nervis lateralibus 6–11, ventraliter inconspicuis. Inflorescentiae 4–9 cm longae; pedunculi pedicellique eglandulares, pedicellis gracilibus, 0.5–1.8 cm longis; flos 1.4–1.8 cm longus; calyx pilosus, tubo 3–4 mm longo, lobulis acutitriangularibus, 3–6 mm longis; corolla lutea; petala subaequalia; vexillum callositatibus pulviniformibus in base laminae distinctis instructis; petala carinae falcata, 8 mm lata, in apicibus acuminata. Legumen lineare, torulosum, 5–16.5 cm longum, 6–7 mm latum, coriaceum, canescenti-sericeum vel subglabrum. Semina lenticularia, pusilla, castanea.

"Ebano" (Estelí, Nicaragua).

Arbustos a árboles pequeños hasta de 6 m de alto; la corteza se defolía en las ramas delgadas; ramas seríceas, pronto glabras, con lenticelas orbiculares a elípticas, cremas. Hojas imparipinnadas estipuladas; estípulas persistentes, aleznadas a casi aciculares, 3–4 mm de largo; pecíolo profundamente canaliculado, (0.5–)1.5–2.5 cm de largo; raquis foliar tereticaule, no alado, canaliculado como el pecíolo, velutino o seríceo hasta glabrescente, (1.5–)3–5.5(–8.5) cm de largo; hojas (7–)9–15-folioladas; folíolos estipelados, estipelas persistentes, aciculares, 1–2 mm de largo; pulvínulos 1–1.5 mm de largo, densamente tomentosos a glabrescentes; láminas cartáceas a subcoriáceas, con los márgenes revolutos, elípticas, (1–)2.5–5.5 cm de largo, (0.5–)1.5–2.5 cm de ancho, ápice agudo a obtuso, mucronado a emarginado, brillantes a opacas y esparcidamente canescente seríceas en el haz y opacas y densamente a esparcidamente canescente velutinas o seríceas en el envés, vena primaria realzada en el envés, laterales 8–11, inconspicuas. Inflorescencias racemosas, laxas, 3.5–9 cm de largo; pedúnculos y pedicelos eglandulares; pedicelos delgados, 0.5–1.8 cm de largo; bráctea floral triangular aleznada, 3 mm de largo. Flores 1.4–1.8 cm de largo; cáliz ligeramente zigomorfo, piloso, su tubo 4 mm de largo, lóbulos triangular agudos, 3–6 mm de largo; corola amarilla; pétalos subiguales en longitud; estandarte con dos callosidades pulviniformes bien marcadas en la base de la lámina; pétalos de la quilla falcados, 8 mm de ancho, ápices acuminados; gineceo seríceo a glabrescente. Legumbre linear, torulosa, 5–16.5 cm de largo, 6–7(–9) mm de ancho, coriácea, inicialmente canescente sericea posteriormente glabrescente; semillas lenticulares, 5 mm de diámetro, 2 mm de grueso, color castaño.

Distribución. En el NO de Nicaragua, de Estelí a Boaco, en selvas sub a caducifolias, bosques de galería y sabanas, asi como en áreas perturbadas; en altitudes entre 400 y 1,000 m. Florece de abril a junio, habiendo un reporte en agosto, fructifica de fines de mayo a julio, persistiendo frutos hasta noviembre.

NICARAGUA. ESTELÍ: Isiqui, *A. Laguna 396* (MEXU, MO); La Gavilana, 13°03′N, 86°19′O, *P. P. Moreno 21881* (MEXU, MO); El Salto, La Estanzuela, 13°02′N, 86°22′O, *M. Sousa et al. 12986* (MEXU, MO). JINOTEGA: a 7 km a la entrada del camino viejo a Jinotega "El Eden", 12°58′N, 85°58′O, *S. Vega & W. Robleto 104* (MEXU, MO). MATAGALPA: Cerro Apante, *P. P. Moreno 132* (MEXU, MO); Darío, El Ojo de Agua, a 12 km de la Carretera Panamericana, 12°46′N, 86°00′O, *Moreno 9320* (MEXU, MO); Darío, a 9 km de la Carretera Panamericana, sobre la carr. a Terrabona, 12°45′N, 86°01′O, *Moreno 9328* (MEXU, MO); Darío, Valle el Jícaro, carr. a Terrabona, a 6 km de la Carretera Panamericana, 12°45′N, 86°03′O, *Moreno 9259* (MEXU, MO); 1.1 km al SO de la bifurcación del Río Grande de Matagalpa, en el camino a Terrabona, 12°38′N, 86°01′O, *W. D. Stevens 9820* (MEXU, MO); a lo largo del camino entre Waswalí Abajo y Waswalí Arriba, 12°55′–56′N, 85°57′O, *Stevens 20311* (MEXU, MO). BOACO: San José de Los Remates, "La Majada", 12°37′N, 85°51′O, *Moreno 16295, Stevens 22279* (MEXU, MO).

Esta especie pertenece al grupo *Madrensis* Rydberg (1924), con hojas imparipinnadas, estandarte con callosidades bien definidas y pétalos de la quilla acuminados, se diferencia de las otras de su grupo: por ser plantas eglandulares; hojas con ápices redondeados, márgenes revolutos; pulvínulos cortos y la pelosidad más densa tanto en hojas, raquis, pulvínulos y frutos. Especie cuya variación más extrema se encuentra en el Cerro Apante, del cual su epíteto deriva.

Coursetia elliptica M. Sousa & Rudd, sp. nov. TIPO: Costa Rica. Guanacaste: A 16 km al NE de Liberia y a 4 al SO de San Jorge, 27 enero de 1983, *M. Sousa 12732, L. D. Gó-*

FIGURE 5. *Coursetia apantensis.*—a. Rama vegetativa.—b. Estipelas y pulvínulos.—c. Rama con inflorescencia.—d. Cáliz.—e. Estandarte.—f. Ala.—g. Quilla.—h. Androceo diadelfo.—i. Gineceo. Tomado de *Moreno 175.*

mez, G. Davidse, C. Humphries, R. Hampshire, N. Garwood & M. Gibby (holotipo, MEXU; isotipos, BM, CR, MO). Figure 6.

Arbusculae, foliis imparipinnatis, (5–)7–9-foliolatis; stipulae persistentes, subulatae vel paene aciculares; rhachis tereticaulis, non alata, canaliculata; foliola, stipellis persistentibus, acicularibus; pulvinuli paene glabri; laminae ellipticae, (1.5–)2.2–5(–6.5) cm longae, (0.5–)1.2–2.5(–3.2) cm latae, ventraliter glabrae, dorsaliter canescenti-sericeae, nervis lateralibus 8–12, dorsaliter inconspicuis. Inflorescentiae 2–6 cm longae; pedunculi pedicellique eglandulares, pedicellis gracilibus, 0.5–1.5 cm longis; flos 1.7–2.3 cm longus; calyx canescenti-sericeus, tubo 3–4 mm longo, lobulis deltoideis vel acutitriangularibus, 3–8 mm longis; corolla lutescens vel albida, vexillo in superficie externa rubrescenti; petala subaequalia; vexillum duobus callositatibus linguiformibus in base laminae bene distinctis instructum; petala carinae falcata, 5–10 mm lata, in apicibus acuminata. Legumen lineare, torulosum, 4–16 cm longum, 5–7 mm latum, coriaceum, glabrum. Semina lenticularia, pusilla, castanea.

Arboles pequeños, hasta 7 m de alto; la corteza se defolia en las ramas delgadas; ramas esparcidamente seríceas, pronto glabras, con numerosas lenticelas orbiculares, cremas. Hojas imparipinnadas; estípulas persistentes, aleznadas a casi aciculares, 2–4.5 mm de largo; pecíolo profundamente canaliculado, (0.5–)1.5–2.5(–3.5) cm de largo; raquis foliar tereticaule, no alado, canaliculado como el pecíolo, esparcidamente seríceo a glabrescente, (2–)3.5–6(–8.5) cm de largo; hojas (5–)7–9-folioladas; folíolos estipelados, estipelas persistentes, aciculares, 2–3.5 mm de largo; pulvínulos (1–)2–3 mm de largo, casi glabros; láminas membranosas a cartáceas, (1.5–)2.2–5(–6.5) cm de largo, (0.5–)1.2–2.5(–3.2) cm de ancho, con los márgenes planos, elípticas, ápice de agudo a obtuso, mucronado a emarginado, brillantes a opacas y glabras en el haz y opacas y canescente seríceas en el envés, vena primaria realzada en el envés, laterales, 8–12, inconspicuas. Inflorescencias racemosas, axilares, laxas, más cortas que las hojas, 2–6 cm de largo; pedúnculos y pedicelos eglandulares; pedicelos delgados, 0.5–1.5 cm de largo; bráctea floral triangular aleznada, 1.5–3 mm de largo. Flores 1.7–2.3 cm de largo; cáliz ligeramente zigomorfo, seríceo, su tubo 3–4 mm de largo, lóbulos deltoides a triangular agudos, 3–8 mm de largo; corola amarillo pálida a blanquecina, el estandarte rojizo en su cara externa, en su cara interna con una guía de nectario verdosa en su base; pétalos subiguales en longitud; estandarte con dos callosidades lingüiformes bien marcadas, arriba de la base de la lámina; pétalos de la quilla falcados, 5–10 mm de ancho, ápices acuminados; gineceo seríceo. Legumbre linear, torulosa, 4–16 cm de largo, 5–7 mm de ancho, coriácea, glabra; semillas lenticulares, 3.5–4.5 mm de diámetro, 2 mm de grueso, color castaño.

Distribución. En las vertientes del Pacífico de Nicaragua y Costa Rica, en selvas medianas caducifolias a subcaducifolias y encinares tropicales; del nivel del mar hasta 580 m. Florece de enero a marzo, habiendo un reporte en junio; fructifica de enero a julio.

NICARAGUA. MANAGUA: S of Managua, *J. M. & M. T. Greenman 5736* (MO); 6 km N-NO de la Carretera 12, a lo largo del camino a la Sierra de Mateare, 12°07′N, 86°24′O, *Stevens 6176* (MEXU, MO); Managua, Loma de Villa Fontana, 12°06′N, 86°16′O *Stevens 21450* (MEXU, MO). GRANADA: Isla Zapatera, Ensenada Los Chiqueros, entre Santa María y ladera O de Laguna de Zapatera, 11°45′N, 85°51′O, *J. C. Sandino 1843* (MEXU, MO); idem, entre Ensenada Los Chiqueros y El Carrizal; sobre el camino a Sonzapote, *Sandino 1887* (MEXU, MO). RIVAS: Puerto San Jorge, *M. & S. Calderón 92* (MO).

COSTA RICA. GUANACASTE: Questa, Parque Nacional de Santa Rosa, *R. Liesner 4552* (CR, MO); Llano Jicacal, Parque Nacional de Santa Rosa, *M. Sousa et al. 12687* (BM, CR, MEXU, MO); a 3 km al E de Cuajinicuil y 11 km del Parque Murciélago, *Sousa et al. 12719* (BM, CR, MEXU, MO); Playa El Hachal, en la Bahía de Santa Elena, *Sousa et al. 12728* (BM, CR, MEXU, MO); 5 km al S de La Cruz, *L. O. & T. P. Williams 24521* (F, MEXU).

Coursetia elliptica también pertenece al grupo *Madrensis* Rydberg y es semejante a *C. apantensis,* pero tiene hojas con menor número de folíolos y márgenes planos; pulvínulos largos; cáliz seríceo con pelos adpresos y en general la pelosidad tanto de hojas y frutos es más rala; su floración ocurre en períodos diferentes, asi como sus rangos altitudinales y distribución geográfica. El nombre de la especie es por la forma elíptica de sus folíolos.

Coursetia paucifoliolata M. Sousa, sp. nov. TIPO: Nicaragua. Dept. Estelí: En el camino Condega a Yalí, 16.9 km NE de la Carretera 1 y a 3.5 km SE del Valle Santa Rosa (13°23′N, 86°17′O), 19 noviembre de 1979, *W. D. Stevens 15813* (holotipo, MEXU: isotipo, MO). Figure 7.

Frutices vel arbusculae, foliis imparipinnatis, 3–5-foliolatis; stipulae persistentes, subulatae vel paene aciculares; rhachis tereticaulis, non alata, canaliculata; foliola stipellis persistentibus, acicularibus; pulvinuli glabrescentes; laminae ellipticae vel anguste ellipticae, lanceolatae, apice acutae vel caudatae, (1.5–)3–6(–7.5)

FIGURE 6. *Coursetia elliptica.*—a. Rama florífera.—b. Cáliz.—c. Estandarte.—d. Ala.—e. Quilla.—f. Androceo diadelfo.—g. Gineceo.—h. Infrutescencia. Las hojas y flores fueron tomadas de *Stevens 9820* y los frutos de *Stevens 20311.*

FIGURE 7. *Coursetia paucifoliolata.*—a. Rama florífera.—b. Apice del raquis, mostrando estipelas y pulvínulos.—c. Cáliz.—d. Estandarte.—e. Base de la lámina del estandarte, mostrando las callosidades.—f. Ala.—g. Quilla.—h. Androceo.—i. Gineceo.—j. Infrutescencia. Las hojas, inflorescencias y flores de *Stevens 15813*, la infrutescencia de *Stevens 16055*.

cm longae, (0.5–)1.5–2.8(–3.5) cm latae, ventraliter nitidae glabraeque, dorsaliter opacae glabrescentesque, nervis lateralibus 4–7 in dorso subelevatis. Inflorescentiae breviores vel longitudini foliorum aequales, 2–7.5 cm longae; pedunculi pedicellique eglandulares, pedicellis gracilibus, 0.5–2.3 cm longis; flos 1.9–2.2 cm longus; calyx sparsim sericeus, tubo 5 mm longo, lobulis deltoideis, 2.4 mm longis; corolla lutescens vel albida, praeter vexillum in superficie externa purpureum, petalis subaequalibus; vexillum duobus callositatibus linguiformibus in basi laminae bene distinctis instructum; petala carinae falcata, 7 mm lata, in apicibus acuminata. Legumen lineare, torulosum, 4.5–6.5 mm longum, 5–7 mm latum, coriaceum, glabrum. Semina lenticularia, pusilla, castanea vel nigricantia.

Arbustos o árboles pequeños; la corteza se defolia en las ramas delgadas, ramas esparcidamente seríceas, pronto glabras, con lentícelas orbiculares, cremas. Hojas imparipinnadas, estipuladas; estípulas persistentes, aleznadas a casi aciculares, 3–7 mm de largo; pecíolo profundamente canaliculado, 1–2.5 cm de largo; raquis foliar tereticaule, no alado, canaliculado como el pecíolo, seríceo a glabrescente, 1–2 cm de largo, hojas 3–5-folioladas; folíolos estipelados, estipelas persistentes, aciculares, 2.5–3 mm de largo; pulvínulos 3–4 mm de largo, glabrescentes; láminas cartáceas, elípticas a angosto elípticas, lanceoladas, (1.5–)3–6(–7.5) cm de largo, (0.5–)1.5–2.8(–3.5) cm de ancho, con los márgenes planos, ápice de agudo a caudado, mucronado, brillantes y glabras en el haz y opacas y glabrescentes en el envés, vena principal y secundarias ligeramente realzadas en el envés, laterales 4–7. Inflorescencias racemosas, laxas, de más cortas a de igual longitud que las hojas, 2–7.5 cm de largo; pedúnculos y pedicelos eglandulares; pedicelos delgados, 0.5–2.3 cm de largo, bráctea floral triangular aleznada, 2 mm de largo. Flores 1.9–2.2 cm de largo; cáliz ligeramente zigomorfo, esparcidamente seríceo, su tubo 5 mm de largo, lóbulos deltoides, 2–4 mm de largo; corola amarillo pálida a blanquecina, el estandarte púrpura en su cara externa, en su cara interna con una guía de nectario oscura verdosa en su base; pétalos subiguales en longitud; estandarte con dos callosidades lingüiformes, bien marcadas, en la base de la lámina; pétalos de la quilla falcados, 7 mm de ancho, ápices acuminados; gineceo seríceo. Fruto linear toruloso, 4.5–6.5 cm de largo, 5–7 mm de ancho, coriáceo, glabro, largo a corto atenuado hacia la base; semillas lenticulares, 4–5 mm de diámetro, 2 mm de grueso, de castaño a casi negras.

Distribución. Sólo del NO de Nicaragua, en dos departamentos, en altitudes entre 540 y 1,300 m. Florece y fructifica en noviembre y diciembre, habiendo un reporte en mayo y persistiendo los frutos hasta febrero.

NICARAGUA. MADRIZ: El Rodeo, 4 km S de Somoto, 13°26′N, 86°34′O, *P. P. Moreno 20082* (MEXU, MO); 2.1 km N de la Carretera 1, en el camino a Palacagüina, 13°27′N, 86°24′O, *W. D. Stevens 5692* (MEXU, MO); Cerro Quisuca, vertientes S y SO, 13°30′N, 86°31′O, *Stevens 16177* (MEXU, MO); ladera O del cerro Volcán de Somoto, 13°25′N, 86°35′O, *Stevens 16421* (MEXU, MO); Cerro Quisuca, cima y laderas superiores, 13°31′N, 86°31′O, *Stevens 16055* (MEXU, MO), *17321-a* (MO). ESTELÍ: El Chayote, 13°16′N, 86°20′O, *Moreno 22799* (MEXU, MO).

Coursetia paucifoliolata es otra especie del grupo *Madrensis* Rydberg, se distingue por sus pocos folíolos por hoja, el ápice de acuminado a caudado de sus folíolos, poca pelosidad en sus láminas; cáliz seríceo y fruto más corto. El nombre específico hace énfasis en los pocos folíolos por hoja.

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THREE NEW SPECIES OF *SOLANUM* SECTION *GEMINATA* (G. DON) WALP. (SOLANACEAE) FROM PANAMA AND WESTERN COLOMBIA[1]

SANDRA KNAPP[2]

ABSTRACT

Three new species of *Solanum* are described: **S. darienense** from eastern Panama, **S. unifoliatum** from the low elevation wet forests of the department of Chocó in Colombia, and **S. dolosum** from higher elevations in the department of Valle de Cauca in Colombia. Relationships of these species are discussed.

Solanum section *Geminata* (G. Don) Walp. is one of the largest sections of *Solanum,* with 82 species, most of these Neotropical. They are generally small trees and shrubs, often growing in primary forest understory, an unusual habit in *Solanum.* Characters useful in recognizing the section are 1) difoliate sympodial units with geminate leaf clusters or unifoliate sympodial units, 2) leaf-opposed inflorescences, 3) plants glabrous or with simple uniseriate trichomes, 4) small white or greenish-white flowers, and 5) hard, green fruits at maturity (see Knapp, 1985, 1986 for discussion of these characters). While preparing a monograph of the group, I encountered many new species, both in the field and in the herbarium. Three of these are described here so that the names can be used in floristic works.

Solanum darienense S. Knapp, sp. nov. TYPE: Panama, Darién, Cana near Río Setigandí, 540–580 m, 18 Apr. 1980, *Gentry et al. 28541* (holotype, MO, location of isotypes unknown). Figure 1.

Frutex; *caules juniores* sparse pubescentes, laete alati; *caules veteres* glabri, cortice nitido rubro-stramineo; *nodi* unifoliati; *folia* elliptica vel ovata utrinque glabra; apice acuto, basi truncata; *inflorescentiae* foliis oppositae simplices filiformes minute puberulae; *pedicelli* sub anthesi filiformes deflexi; *calycis lobi* deltoidei minute puberuli; *corolla* alba lobis sub anthesi reflexis; *bacca* globosa viridis, pedicello frugifero deflexo ad apicem expanso; *semina* fusca ovoidea reniformia, testa foveolata.

Shrubs with foetid foliage, 1–1.5 m tall; young stems sparsely hispidulous with erect uniseriate trichomes ca. 0.1 mm long, these often only on one side of the stem; young leaves glabrous; stems winged from the decurrent leaf bases; bark of older stems reddish-golden and shiny. Leaves elliptic to ovate, not geminate except on non-reproductive nodes, widest at or just below the middle, glabrous on both surfaces, occasionally minutely puberulent along the veins beneath, 11–14 cm long, 3–4.5 cm wide, with 7–8 pairs of primary veins, these not prominently raised above, prominent and yellowish beneath, the apex acute to acuminate, the base truncate; petioles winged from the decurrent leaf bases, ca. 1 mm long. Inflorescences opposite the leaves, simple, thread-like, 0.5–1.5 cm long, 4–5-flowered, minutely puberulent with erect uniseriate trichomes like those of the stems; pedicel scars evenly spaced 1–2 mm apart, slightly raised; pedicels at anthesis filiform, 0.6–1 cm long, tapering from the calyx to a slender base ca. 0.25 mm in diameter, sparsely puberulent with uniseriate trichomes; buds globose when young, hispidulous with uniseriate trichomes like those of the rest of the inflorescence, the corolla soon exserted from the calyx tube making the buds elliptic to obovoid; calyx tube broadly conical, ca. 0.5 mm long, the lobes deltoid, 0.25–0.5 mm long, the margins paler, the lobes and tube minutely hispidulous with uniseriate trichomes ca. 0.1 mm long; corolla white, 5–7 mm in diameter, lobed nearly to the base, the lobes reflexed at anthesis, the tips and margins of the lobes minutely papillose; anthers ca. 1.5 mm long, 1 mm wide, poricidal at

[1] I thank James Mallet, W. G. D'Arcy, and Michael D. Whalen for advice and encouragement; Bente Starke King for the illustrations; and the curators of the following herbaria for the loan of specimens or the use of facilities, BH, COL, F, MO, NY, US. This research was funded by U.S. National Science Foundation grant BSR 8302773 to Michael D. Whalen and Sandra Knapp, and by an American Association of University Women Educational Foundation Fellowship to Sandra Knapp.

[2] L. H. Bailey Hortorium, 467 Mann Library, Cornell University, Ithaca, New York 14853.

FIGURE 1. *Solanum darienense* (from *Gentry et al. 28541*), scale bar equals 1 cm.

the tips, the pores becoming slit-like upon drying; free portion of the filaments 0.25–0.3 mm long, the filament tube ca. 0.1 mm long; ovary glabrous; style straight, 3–3.5 mm long; stigma a slight broadening at the top of the style, minutely papillose. Berries globose, green at maturity, ca. 1.5 cm in diameter; fruiting pedicels deflexed, woody, 1.8–1.9 cm long, expanded at the apex, 0.5–0.75 mm in diameter at the base; seeds dark brown in dry material, ovoid-reniform, 3–3.5 mm long, 2–2.5 mm wide, the surfaces minutely pitted. Chromosome number: not known.

Distribution. In the low mountains of eastern Panama, the only collections are from the vicinity of the gold mine at Cana, from 500 to 600 m elevation. Figure 2.

Solanum darienense is related to *S. confine* Dunal in DC., a species of the Andean foothills in eastern Peru, and to *S. pertenue* Morton & Standley of montane Costa Rica and western Panama. *Solanum darienense* is distinct from these two species in its reddish-golden bark, slightly winged stems, obtuse, slightly oblique leaf bases and generally glabrous leaves. The members of this species complex are all very similar, perhaps due to their primary forest habitat. D'Arcy (1973) recognized *S. darienense* as a new entity from Panama but, due to the paucity of material available at the time, did not describe it. The species may also occur in adjacent Colombia or in other parts of the range of low mountains on the Panama-Colombia border.

Additional specimens examined. PANAMA. DARIEN. Vicinity of airstrip at Cana gold mine, 480 m, 29 Jul. 1976, *Croat 37963* (MO); vicinity of Cana, 1,750 ft, 23 Jun. 1959, *Stern et al. 477, 661* (MO, US).

Solanum unifoliatum S. Knapp, sp. nov. TYPE: Colombia, Chocó, Municipio de Chocó,

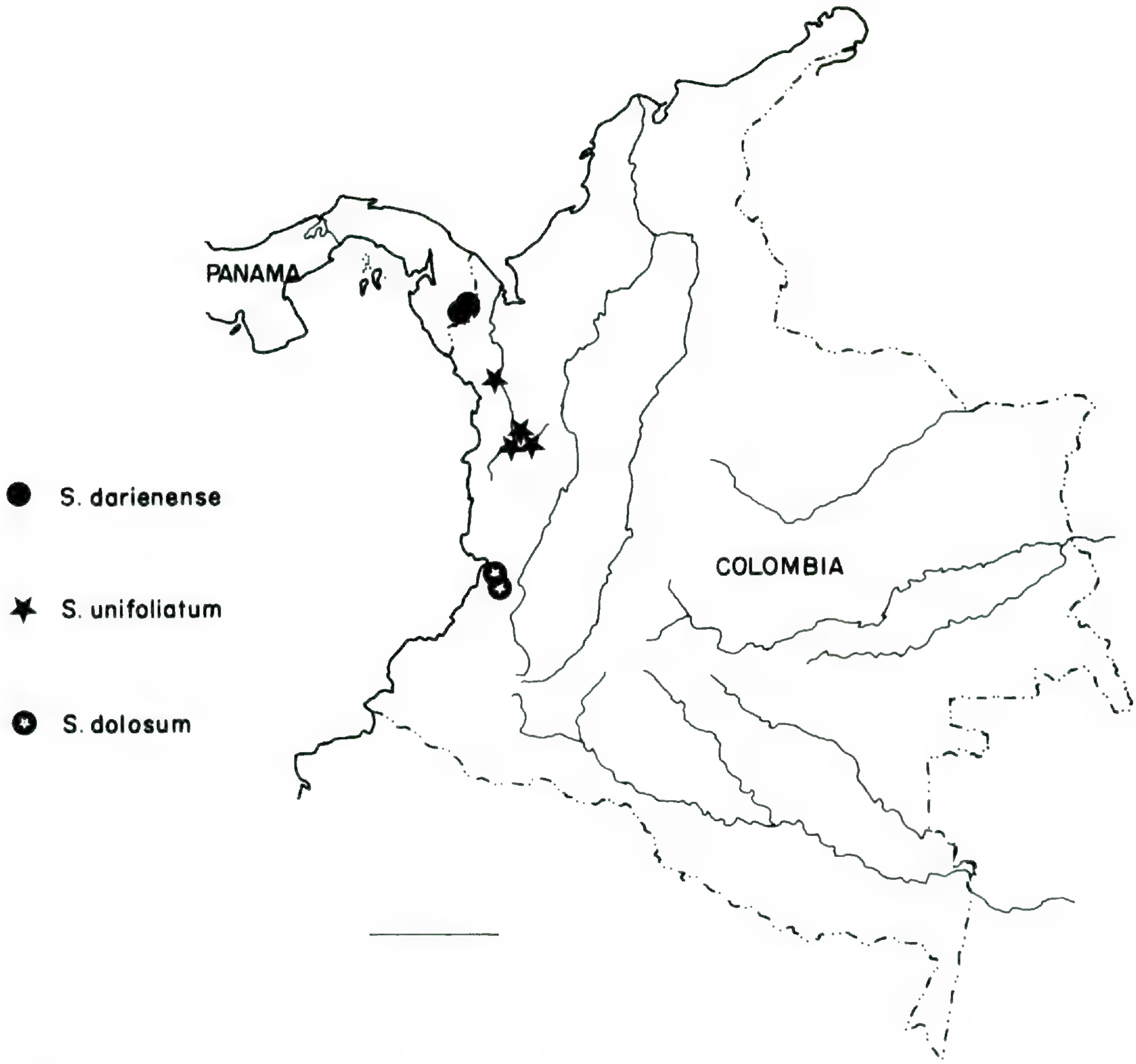

FIGURE 2. Distribution of *S. darienense, S. unifoliatum,* and *S. dolosum,* scale bar equals 200 km.

Carretera Quibdó-Tutenendo 15 km de Quibdó, 45 m, 6 Sep. 1976, *Forero & Jaramillo 2544* (holotype, MO, isotype, COL, not seen). Figure 3.

Frutex; *caules* glabri laete alati, cortice viridi-fusco; *nodi* unifoliati; *folia* elliptica vel anguste elliptica utrinque glabra, apice longe acuminato, basi attenuata, marginibus revolutis undulatis; *inflorescentiae* foliis oppositae simplices, cicatricibus pedicelli arcte et aequaliter dispositis; *pedicelli* sub anthesi deflexi filiformes; *calycis lobi* irregulariter rotundati; *corolla* minuta pallide viridis, lobis sub anthesi reflexis; *bacca* globosa viridis, pedicello frugifero erecto vel deflexo.

Shrubs or subshrubs, 1–3 m tall; stems glabrous, lightly winged between the nodes with the decurrent leaf bases; bark light greenish brown, sparsely lenticellate, in age becoming paler and exfoliating. Sympodial units unifoliate. Leaves elliptic to narrowly elliptic, not geminate, widest at the middle, glabrous on both surfaces, 18.8–27.5 cm long, 4.8–7.3 cm wide, with 5–6 pairs of primary veins, only the midrib raised above, prominent below, the apex long acuminate, the base attenuate, winged onto the petiole and the stem; margins revolute and slightly undulate, occasionally somewhat erose; petioles 2–2.6 cm long, winged from the decurrent leaf bases. Inflorescences opposite the leaves, simple, 0.6–3 cm long, 20–100-flowered, sparsely papillose distally; pedicel scars closely and evenly packed, but not overlapping; pedicels at anthesis 5–6 mm long, deflexed, filiform, less than 0.25 mm in diameter at the base, abruptly widening to the calyx tube; buds globose, translucent, minutely

FIGURE 3. *Solanum unifoliatum* (from *Forero & Jaramillo 2808* & *Gentry & Fallen 17585*), scale bar equals 1 cm.

papillose; calyx tube ca. 0.5 mm long, cup-shaped, the lobes rounded and irregular, ca. 0.5 mm long, minutely papillose; corolla minute, pale green, ca. 5 mm in diameter, lobed three-quarters of the way to the base, the lobes reflexed at anthesis, the tips and margins of the lobes minutely papillose; anthers ca. 1.5 mm long, 0.5 mm wide, poricidal at the tips, the pores becoming slit-like upon drying; free portion of the filaments less than 0.1 mm long, the filament tube less than 0.1 mm long; ovary glabrous; style straight, ca. 2.5 mm long, in short styled flowers ca. 0.5 mm long; stigma clavate, dark papillose at the tip. Berries globose, slightly umbonate when immature, green at maturity, 0.8–1 cm in diameter; fruiting pedicels erect or somewhat deflexed,

woody, 1.8–2 cm long, 0.5–1 mm in diameter at the base; immature seeds flattened-reniform, ca. 2 mm long, 2 mm wide, the surfaces minutely pitted. Chromosome number: not known.

Distribution. Found only in the pluvial forest in the department of Chocó in Colombia, near sea level. All known collections are from the upper Rio Atrato basin. Apparently a plant of both primary and secondary forest. Figure 2.

Solanum unifoliatum is very closely related to *S. triplinervium* Morton, also of the Chocó floristic province but known only from Isla Gorgona off the department of Nariño. The two species share unifoliate nodes, unusual in the section, crowded inflorescences with closely packed pedicel scars, and large glabrous leaves. *Solanum unifoliatum* differs from *S. triplinervium* in its longer inflorescences and leaf venation. *Solanum triplinervium,* as the name suggests, has three main veins from the leaf base, and the strongly parallel tertiary venation is very like that of a member of the Melastomaceae (Morton, 1944). *Solanum unifoliatum* has leaf venation like other members of the Solanaceae.

Only two flowers are present on the type specimen, and one of these is apparently short-styled. Andromonoecy has not been demonstrated in section *Geminata,* but this is one of the many species with short and long-styled flowers. The large numbers of fruit set on each inflorescence of *S. unifoliatum* seems to indicate that the species is not andromonoecious (see Whalen & Costich, 1986), but further work is clearly needed.

Additional specimens examined. COLOMBIA. CHOCÓ. Quibdo, Guayabal, Rio Hugon, ca. 80 m, 12 Sep. 1976, *Forero & Jaramillo 2808* (MO); 7 km W of Tutenendo on road to Quibdo, ca. 100 m, 12 Aug. 1976, *Gentry & Fallen 17585* (MO); 11 km S of Quibdó on road to Yuto, ca. 50 m, 7 Jan. 1979, *Gentry & Renteria A. 23726* (MO); road from Lloro to Yuto, ca. 2 km E of Yuto, ca. 50 m, 18 Jan. 1979, *Gentry & Renteria A. 24410* (MO, NY).

Solanum dolosum Morton ex S. Knapp, sp. nov. TYPE: Colombia, Valle de Cauca, Cordillera Occidental, La Cumbre, 1,600–1,800 m, 14–19 May 1922, *Killip 5705* (holotype, US, isotype, NY). The sheet at US bears an annotation label in Morton's handwriting dated Nov. 1935 stating "*Solanum dolosum* Morton TYPE", but a description was never provided for this species. This sheet is therefore designated as the holotype. Figure 4.

Frutex; *caules juniores* pubescentes valde alati; *nodi* unifoliati; *folia* lanceolata vel linearia supra glabra subtus secus nervos puberula, apice longe acuminato, basi cuneata, marginibus erosis ad apicem ciliatis; *inflorescentiae* foliis oppositae vel internodaliae simplices pubescentes; *pedicelli* sub anthesi deflexi; *calycis lobi* deltoidei in alabastro carnosi; *corolla* alba, lobis longe acuminatis sub anthesi reflexis; *bacca et semina* ignotae.

Shrubs or climbing shrubs, of unknown height; young stems and leaves hirsute with unseriate golden trichomes ca. 0.1 mm long; the ultimate branchlets slender; bark of the older stems partially glabrate, golden green; stems strongly winged from the decurrent leaf bases, and also from *de novo* wings arising ca. 1 mm below the inflorescence. Sympodial units unifoliate. Leaves lanceolate to linear, not geminate, widest just below the middle, 5.5–11.2 cm long, 1.4–1.7 cm wide, with 6–10 pairs of primary veins, these indistinct above except for the raised midrib, prominent, yellowish, and puberulent with uniseriate trichomes 0.05–0.1 mm long, the apex long acuminate, the extreme tip blunt and rounded, the base cuneate, decurrent on the petiole and stem; the leaf margins erose, ciliate near the apex; petioles winged, 1–5 mm long. Inflorescences opposite the leaves or occasionally internodal, filiform, simple, 0.5–1.2 cm long, 2–6-flowered, densely to sparsely hirsute with uniseriate golden trichomes like those of the young leaves and stems; pedicel scars irregularly spaced 0.5–2 mm apart, beginning 2–3 mm from the base of the inflorescence; pedicels at anthesis 4–6 mm long, deflexed, tapering from the calyx tube to a slender base ca. 0.5 mm in diameter, sparsely pubescent with uniseriate trichomes; buds globose, the calyx lobes swollen and knob-like; calyx tube ca. 1 mm long, sparsely pubescent, the lobes broadly deltoid, 0.5–1 mm long, sparsely pubescent with the same golden uniseriate trichomes as the rest of the inflorescence, minutely papillose at the tips; corolla white, 8–9 mm in diameter, lobes three-quarters of the way to the base, the lobes long acuminate, reflexed at anthesis, minutely papillose on the tips and margins; anthers 1.5–2 mm long, the terminal ca. 0.2 mm thickened and paler, 1–1.5 mm wide, poricidal at the tip, the pores becoming slit-like upon drying; free portion of the filaments 0.5–1 mm long, the filament tube ca. 1 mm long; ovary glabrous; style straight, ca. 4 mm long; stigma not distinguishable from the rest of the style, minutely papillose on the extreme tip. Ber-

FIGURE 4. *Solanum dolosum* (from *Killip 5705, 11589*), scale bar equals 1 cm.

ries globose, glabrous, only immature ones seen. Chromosome number: not known.

Distribution. On the western slopes of the Cordillera Occidental in the department of Valle de Cauca in Colombia, from 1,200 to 2,000 m in elevation. Figure 2.

Solanum dolosum is most closely related to an undescribed species from high elevation eastern

Bolivia. It shares with that species leaves that are ciliate at the apex, filiform inflorescences, and zig-zag stems. The inflorescences of *S. dolosum* are much shorter, ca. 1 cm as opposed to 3–5 cm, and the leaves are acute at the base. *Solanum dolosum* is also quite similar to *S. longevirgatum* Bitter, also found on the western slope of the Cordillera Occidental, but from higher elevations in the department of Cauca. *Solanum dolosum* is distinct from *S. longevirgatum* in its lanceolate to linear leaves that are ciliate at the apex, shorter pubescence, and much smaller (8–9 mm in diameter versus 1–2 cm in diameter) flowers. The two species share unifoliate nodes, fleshy calyx lobes in bud, prominent yellow leaf venation, and erose leaf margins.

Additional specimens examined. COLOMBIA. VALLE DE CAUCA. Cordillera Occidental, W slope, Rio Digua, right bank between Queremal & La Elsa, 1,160–1,200 m, 27, 29 Mar. 1947, *Cuatrecasas 23897* (US); La Cumbre, Cordillera Occidental, 1,600–2,100 m, 25–27 Sep. 1922, *Killip 11589* (NY, US).

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A SURVEY OF *SOLANUM* PRICKLES AND MARSUPIAL HERBIVORY IN AUSTRALIA[1]

D. E. SYMON[2]

ABSTRACT

A survey of the prickliness of *Solanum* in Australia is made and the distribution of the most prickly species is mapped. A survey of the diets of vertebrate herbivores in Australia is presented. It is concluded that the development of prickles is not a response to the physical environment but to browsing by marsupials belonging primarily to the group known as wallabies.

It is commonly asserted (Kerner, 1897; Fritsch & Salisbury, 1953; Davis & Heywood, 1967) that prickles are an adaptation to arid environments or to heavy grazing. If the second assertion is correct, one could expect to find some spacial relationship between the presence of herbivores and the distribution of prickly species. A survey of a large genus displaying varied prickliness over a substantial area may be a way of showing any relationship and is attempted here. The availability of a recent revision of *Solanum* in Australia in which data on the species and their distribution are available (Symon, 1981) enables such a comparison to be made. The genus *Solanum* is not unique in its varied prickliness and occurrence over large parts of Australia; other large genera that might also be surveyed are *Acacia* or *Hakea* but both of these lack comprehensive revisions.

Familiarity with *Solanum* in Australia has lead me to doubt any special relationship between prickles and aridity and a glance at Figure 1 does not indicate any special concentration of prickliness in the most arid areas nor is this supported in Table 2, which shows the distribution of prickly species in relation to moisture index. This aspect will not be followed further here.

The survey is presented in three sections. First, an estimate of prickliness was determined for all species of *Solanum* in Australia and the distribution of the most prickly species was mapped. Second, an extensive survey of the reported diets of herbivores was made in an attempt to discover what animals were significant herbivores and exactly what they ate. An appalling lack of knowledge of diets was revealed but all principal herbivores are discussed in detail. Third, a brief survey is made of exotic *Solanum* species on some islands where vertebrate herbivores are absent.

Two sections of the genus native to Australia are completely unarmed, sect. *Solanum* (Black nightshades) and sect. *Archaesolanum* (Kangaroo apples). The species are small or large shrubs growing mostly well within the range of herbivores. An alternative strategy of plant protection must be operating and in this regard it is notable that the level of alkaloids in these two sections is considerably higher than in the sections with prickly species (Bradley et al., 1978).

MATERIALS AND METHODS

A measure of prickliness for each native *Solanum* species was obtained by counting the number of prickles on 4 cm lengths of stem on herbarium specimens. At least 10 collections of each species were examined (or all that were available in rare species). The lengths of about 50 prickles were measured for each species. Old weathered stems were excluded and where possible a distinction was made between those specimens in juvenile phases of growth and mature specimens. However, few herbarium specimens contain information on the age of the shrub, position of the sample, or details of prickle distribution on the plant.

RESULTS

A total of 83 species was examined (Table 1). Two species were so inadequately represented that no worthwhile estimate was made; *S. ca-*

[1] I am particularly grateful to P. B. Copley and A. C. Robinson for allowing me access to unpublished data on the diet and distribution of *Petrogale xanthopus*, to the latter for advice and assistance on the distribution of many species of marsupials, and to Dr. G. D. Sanson for helping to sort out the browsers and grazers. This paper was part of the Second International Symposium of the Biology and Systematics of the Solanaceae presented at the Missouri Botanical Garden on 3–6 August 1982.

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FIGURE 1. Distribution of the most prickly species of *Solanum*.

taphractum A. M. Cunn. ex Benth. from the north west coast of Western Australia and *S. sporadotrichum* F. Muell. from the Queensland rainforest, and these two will not be discussed further. Six species were unarmed in the specimens available. No prickles were found on *S. densevestitum* F. Muell., *S. nemophilum* F. Muell., or *S. tetrandum* R. Br., and these three are believed to be wholly unarmed. The few specimens of *S. dunalianum* Gaudich that were available were unarmed but it is known from specimens from New Guinea that this species has the potential to produce prickles and a range of juvenile plants and more collections are needed to get any estimate of prickliness. This species is restricted in its distribution in Australia to the far north of Cape York. *Solanum viridifolium* Dunal is a small tree found in the rainforests of Queensland and is unarmed in the many herbarium sheets available. Young plants collected by B. Hyland at Atherton, and plants grown from seed, have sparse weak prickles on the main stem in the juvenile phase and the taxon certainly has the potential to produce prickles although it is completely unarmed when mature. *Solanum tumulicola* Symon is an herbaceous perennial found about Daly Waters in the Northern Territory. It is unarmed in most collections, but a few plants do have some small weak prickles towards the base and, like *S. viridifolium*, the species has the capacity to produce prickles. All other species can be described as prickly to a greater or lesser extent. The lower level of prickliness is represented by *S. esuriale* Lindley, 10 collections from each of Western Australia, Northern Territory, and Queensland had no prickles whereas collections from New South Wales and South Australia averaged about one prickle per 4 cm length. At the other extreme are *S. semiarmatum* F. Muell. from eastern Australia with a mean of 70 prickles per 4 cm length of stem and *S. ashbyae* Symon from Western Australia with 43 prickles.

Several species are conspicuously prickly on the main stem in the juvenile phases of growth and have fewer prickles on mature and distal twigs. Few herbarium specimens represent such species adequately and more may show this characteristic than have been recorded. Conspicuous examples are: *S. inaequilaterum* Domin, 37 below, six above; *S. macoorai* Bailey, 26 below, five above; *S. asymmetriphyllum* Specht, six below, 0.3 above; *S. clarkiae* Symon, 39 below, 21 above. The first two are found in the rainforest of eastern Australia and the second two at the foot of the escarpments in northern Arnhemland. All but *S. clarkiae* will form small treelets, and if the prickles do deter herbivores it is an attractive guess that the later, lightly armed leaves and twigs are out of reach.

In almost all species the stems are more strongly armed than the leaves. No count of prickles per unit leaf area has been made, but *S. lacunarium* from the Darling-Murray river system and with an inland population near Lyndhurst in South Australia has leaves that are more prickly than the stems. Two possible reasons for this difference between stems and leaves may be suggested. Leaves may be more expendable than stems because a leaf once lost may be replaced by a new one but the loss of a stem is more serious damage. Secondly, to be effective prickles are best held rigidly, and flaccid leaves may not be fully effective bases for prickles. In most cases prickles on leaves are concentrated on the stronger main veins and lower portions of the leaf. If leaves are bitten as a mouthful, relatively few prickles may be effective. Little is known of what animals graze *Solanum*, but judged by human impressions many leaves seem ineffectively protected and one would expect a fastidious small grazer to be able to nibble such leaves with relative ease. Although it is true that some degree of prickliness would deter vertebrate herbivores, many species are so lightly armed that the effectiveness of their prickles can be seriously questioned.

Contemporary accounts of the effectiveness of prickles seem to be very sparse. Janzen (1981), in a review of legume defences against herbivores, only mentioned prickles in discussing the

TABLE 1. Prickliness of Australian *Solanum* species. Mean number per 4 cm length of stem and mean length (mm).

		No.	Length (mm)
adenophorum		6.3	3.9
ashbyae		43.3	5.2
asymmetriphyllum	young	6	4.4
	old	0.3	3.3
beaugleholei		24.7	5.0
brownii		4.0	6.0
campanulatum		16.4	4.4
carduiforme		22.3	4.3
centrale		2.0	3.0
chenopodinum		1.5	6.3
chippendalei		14.5	4.1
cinereum		10.0	7.6
clarkiae	young	39.5	4.8
	old	21.0	4.0
cleistogamum	W.A.	18.0	4.9
	N.T.	16.0	3.1
coactiliferum	W.A.	3.7	3.8
	N.T.	2.2	4.1
	N.S.W.	2.4	3.6
	east S.A.	4.3	4.4
	west S.A.	2.1	4.0
cookii		16.6	5.6
corifolium		1.4	5.0
cunninghamii		8.6	2.8
dallachii		0.7	4.6
densevestitum		0	0
dianthophorum		13.7	4.3
dimorphispinum		3.0	4.6
dioicum	King Leopold	8.5	3.1
	Gibb & Hann R.	4.0	3.8
	Tanami Desert	18.4	5.3
discolor		4.8	5.0
diversiflorum		4.4	6.0
dunalianum		0	0
eardleyae		33.9	4.9
eburneum		15.9	4.1
echinatum		9.5	3.5
elachophyllum		4.0	10.5
elegans		2.6	5.9
ellipticum	typical	11.8	4.4
	NT prickly	29.3	6.8
	SW Eyre Pen.	7.8	4.6
eremophilum		8.3	4.2
esuriale	W.A.	0	0
	N.T.	0	0
	Q.	trace	
	N.S.W.	1.1	2.4
	S.A.	0.7	2.5
ferocissimum	N.T.	4.1	4.5
	Q.	4.0	6.1
	N.S.W.	5.2	5.7
furfuraceum		1.4	7.6
gabrielae		3.7	4.0

TABLE 1. Continued.

		No.	Length (mm)
gilesii		6.3	4.8
hamulosum		6.7	3.6
hesperium		4.3	1.6
heteropodium		32.8	4.2
hoplopetalum		24.5	5.2
horridum		40.2	4.9
hystrix		17.1	4.3
inaequilaterum	young	37.4	5.9
	old	6.5	4.8
karsensis		1.6	7.8
lachnophyllum		38.2	4.5
lacunarium	inland	2.1	2.1
	main river	3.5	2.3
lasiocarpum (*ferox*)		15.1	3.0
lasiophyllum	(Giles)	24.1	4.9
	W.A.	16.7	3.2
leopoldensis		16.3	4.3
lucani	W.A.	18.8	3.8
	N.T.	23.7	4.5
macoorai	young	26.1	6.6
	old	5.3	4.1
melanospermum	young	16.0	—
	old	4.0	—
multiglochidiatum		27.0	3.75
nemophilum		0	
nummularium		3.7	6.7
oedipus		40.5	7.0
oldfieldii		3.3	3.5
oligacanthum		4.0	5.6
orbiculatum	ssp. *orbic*	2.0	6.4
	ssp. *macro*	1.9	7.3
papaverifolium		14.1	3.4
parvifolium		4.7	4.7
petraeum		23.4	3.2
petrophilum	(Flinders)	12.5	6.4
phlomoides		19.1	4.3
plicatile		3.4	2.8
prinophyllum		9.1	7.8
puguinculiferum		2.7	9.2
pungetium		3.5	4.8
quadriloculatum		18.0	3.9
seitheae		21.5	3.7
semiarmatum		70.1	3.1
sporadotrichum	(1)	26.0	4.4
stelligerum		1.5	5.3
sturtianum	W.A.	1.3	3.3
	S.A.	0.8	3.3
terraneum		3.3	2.4
tetrandrum		0	
tetrathecum		1.2	7.6
tudununggae		1.2	2.6
tumulicola		0	
vansittarensis		0.7	5.8
viridifolium		0	
yirrkalensis		2.8	3.5

TABLE 2. Distribution of *Solanum* species in relation to the moisture index, summer season (Nov.–April).

Moisture Index Summer Season	Number of Prickles																									
	0	1–2	3–4	5–6	7–8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	—	64
>8	*																									
	*																									
	*	*																								
	*	*	*						*																	
	*	*	*	*					*					*												
	*	*	*	*	*	*			*			*	*	*			*			*	*				—	*
0.6–0.8			*			*			*																	
0.4–0.6					*																					
	*		*			*			*					*												
			*																							
			*											*												
0.2–0.4		*																								
	*													*												
			*		*																					
<0.2		*	*		*		*									*	*									
		*		*		*	*									*										
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ant-thorn *Acacia*. There is no mention of conventional prickles, thorns, pungent leaves, or vertebrate herbivores. Main (1981), in discussing plant responses to herbivory, mentioned nutritional value and toxicity but not tomentum or prickles. Tomlinson (1962), in discussing the prickles of palms, did consider that they are a response to herbivory and gave some interesting information on their origin and distribution.

A Survey of the Published Data on the Diets of Herbivores in Australia

INSECTS

No adequate survey of insect herbivores on *Solanum* is available. Many leaves bear evidence of insect activity. I have observed that flea beetles (Fam. Chrysomelideae), looper caterpillars (Fam. Geometrideae), grasshoppers (Fam. Acridideae), and leafminers (Fam. Tineideae) are all relatively common on species of *Solanum*. No doubt there are many more. The smaller insects, e.g., flea beetles, can move readily between most prickles, and severe leaf damage on some very prickly species (by human standards), e.g., *S. prinophyllum* Dunal, is evidence of this. In some cases dense prickles could conceivably keep large insects off the plant surface, but this must be quite rare and prickly species like *S. oedipus* Symon with well armed leaves and stems are extensively attacked by grasshoppers (pers. obs.). In looking through herbarium specimens I have concluded that apparent insect damage is more closely related to the length and density of the tomentum than to prickliness.

REPTILES

Although a few Australian reptiles (the larger Skinks) are herbivorous, their diet seems restricted to flowers and fruits. I have found none that regularly eat leaves of *Solanum* and they can be disregarded as significant herbivores of these species in Australia.

BIRDS

The two large flightless birds Emu and Cassowary are both herbivorous. The Cassowary is known to eat fruit (Stocker & Irvine, 1983), especially fallen fruit, and is not known to graze to any extent. Its distribution is strictly limited to rainforest areas of northern Queensland and it can scarcely be considered a significant factor in the more extensive browsing of plants.

By contrast, the Emu was extremely widespread and is omnivorous. Fruits, flowers, a wide range of vegetable matter, and insects make up its diet. It certainly eats *Solanum* fruits, even those with prickly calyces (Symon, 1979). Davies (1978) gave details of Emu diets in Western Australia. Within a very wide range of tolerance they take advantage of locally abundant fruit, flowers, herbage, and insects. Shoots and herbage formed an important part from January to October and grasses and Compositae shoots were ranked among the most abundant. The leaves of *S. ashbyae* were eaten in April and August. Davies did not list *Solanum* fruits in his tables or Appendices despite their importance in eastern Australia as cited by Noble (1975). Davies pointed out that Emus prefer succulent food items to dry ones, and such a diet does not include dried herbage or grasses or the mature leaves of shrubs. Three prickly plants provided significant amounts of food, i.e., *Acacia tetragonophylla, A. victoriae,* and *Scaevola spinescens*. In all cases the Emu ate the fruits and may be a dispersal agent rather than predator.

No native mammalian herbivores occurred in New Zealand and the only large vertebrates were the now extinct Moa. Greenwood and Atkinson (1977) suggested that the long-term effect of Moa browsing in New Zealand was the development of a large number of shrubs with an intricate divaricate growth habit, but scarcely any prickly shrubs. This thesis is challenged by McGlone and Webb (1981). The action of an Emu would be of plucking, pulling and breaking; the chewing or nibbling of an ungulate is scarcely possible. I have found no comment on the possible effect of Emus on the morphology of the Australian flora. A few intricate divaricate shrubs occur in Australia, but nowhere in the proportion that they occur in New Zealand. Their number could include *S. nummularium* S. Moore from Western Australia, of which the Emu would eat the ripe berries, rather than pluck the twigs. It is unlikely that the Emu is of significance as a browser of fresh foliage, although their role in seed dispersal is undoubted.

MAMMALS

In Australia mammalian herbivores would have been marsupials and to a lesser extent native rodents. No ungulates were originally native to Australia. The marsupials occur in great array ranging from kangaroos 2 m tall to the smallest wallabies, bandicoots, and possums, some no

larger than a rat, and these must be considered the major herbivores of the Australian flora. Some fossil species were larger than any living species and were considered to be browsers (Sanson, 1978). Because some of these became extinct in relatively recent times, it is likely their influence may still be reflected in the present vegetation.

Family Thylacomyidae, bandicoot. Watts (1969) in a paper on the distribution and habits of the rabbit-eared bandicoot (*Macrotis lagotis*) showed that plant material composed most of the diet and listed *Solanum* seed and *Solanum* roots as items of diet. *Solanum* seed remains in the feces formed 23% of the whole in one sample and in many cases were intact. Although once more widely spread, this bandicoot is now extremely restricted in number and area (an endangered species) and seems unlikely to have been an effective browser on *Solanum*.

Family Phalangeridae, possums. Van Dyck (1979) reported the destruction of wild tobacco tree (*S. mauritianum*) by mountain possums (*Trichosurus caninus*) in south east Queensland. This alien *Solanum* is a small tree, quite unarmed, and the animals ate the leaves and in particular the bark, often stripping the stems to ground level and causing their death. Van Dyck also gave other unpublished reports of the coppery brushtail (*T. vulpecula*) eating this species. Proctor-Gray (pers. comm.) reported that this species also eats the leaves and unripe fruits of *S. seaforthianum*, an unarmed, alien, climbing species. The native rainforest species of *Solanum* are rarely robust enough to sustain the weight of the possums, but their densely prickly main stems could reduce predation and protect the bark. Possums do not now occur over large areas of Australia, they are largely arboreal, and few *Solanum* in Australia are robust enough to sustain them. Freeland and Winter (1975) in a study of the brushtail possum (*T. volpecula*) reported that this species spent up to 23% of its feeding time on the ground and that the animals "probably" ate the leaves of *S. nigrum* (?*S. americanum*), an unarmed species. Possums eat unarmed introduced *Solanum* but have not been reported eating prickly native species.

Family Petauridae, possums and gliders. No data located.

Family Macropodideae, kangaroos and wallabies. Sanson (1978), on the basis of mastication characteristics, divided the Macropodidae into a browsing grade and a grazing grade. The first was considered ancestral and included those genera whose diet was substantially of soft, unabrasive, low fibre plant, whereas the latter was a derived grade specialised to eat the more abrasive, siliceous, high fibre grasses. The browsers included *Wallabia bicolor* (swamp wallaby), *Setonix brachyurus* (quokka), *Thylogale* spp. (pademelon), *Dendrolagus* spp. (tree kangaroo), *Lagostrophus* (hare wallaby), the New Guinea genera *Dorcopsis, Dorcopsulus,* and the extinct genera *Protemnodon, Hadronomas, Dorcopsoides,* and *Sthenurus.* An intermediate grade includes *Petrogale* (rock wallaby) and the fossil *Troposodon.*

The grazing grade included *Onychogalea* (nailtail wallaby), *Lagorchestes* (hare wallaby), many, but not all of *Macropus/Megaleia* (kangaroo and euro), and the fossil *Peradorcas, Fissuridon,* and *Procoptodon.* In his (1978) paper, Sanson did not give specific names and the species included in his genus *Prionotemnus* are not stated. For this study and from Sanson (1980), I have considered *Macropus bernardus, M. fulginosus, M. giganteus, M. parma, M. parryi, M. rufogriseus,* and *M. rufus* to be grazers and *Macropus agilis, M. dorsalis, M. eugenii* and *M. robustus* to be intermediate; *M. irma* is inadequately known and *M. greyi* is now extinct.

Sanson believed that the browsers did not consume large quantities of grasses, that extant browsers tend to show relict patterns of distribution, and that the oldest fossil members of the Macropodideae were all browsers. In contrast, the advanced grazers are distributed in recently developed arid and savannah grassland regions. Increasing aridity, the extinction of denser wet forests in the central regions of Australia, and an increase in grassland and shrub steppe at the end of the Miocene provided the impetus for change.

Bolton and Latz (1978) make no mention of *Solanum* in the brief list of plants eaten by the western hare-wallaby (*Lagorchestes hirsutus*). The diet given, though admittedly inadequate, suggests a grazer rather than a browser.

Christensen (1980), in a study of the woylie (*Bettongia penicillata*), showed that fungi composed a significant proportion of its diet throughout the year. Some starchy and cellular material was present but no mention was made of leafy herbage. No mention was made of *Solanum* in the diet or in the environment (likely to be rare in that area) and the woylie does not appear to be a significant herbivore of leafy material.

Stocker (1982) reported that the red-legged pademelon (*Thylogale stigmatica*) is active in stripping and eating the bark from the lower 50

cm of the alien *Solanum mauritianum* to the extent that the tops may be killed, though the base may coppice. This species is quite unarmed.

George (1982) stated that "the tree kangaroo (*Dendrolagus*) spends much of its time on the ground and presumably feeds predominantly on ground herbage." No precise details of its diet appear to be available.

Storr (1964) in a study of the quokka (*Setonix brachyurus*) on Rottnest Island, Western Australia recorded *Solanum simile* as a minor item of diet in January to March. The maximum percentage of the diet recorded comprising *Solanum* was 12%. This *Solanum* is quite unarmed. From the list of plants eaten it appears that the quokka is a browser rather than a grazer. Elsewhere Storr (1962) stated "the leaves, young stems and bark off older stems are only eaten in areas where little or no other herbage is available. Ripe fruits are eaten in summer and autumn. Ordinarily the plant is not important as food, it is more valuable as shelter when growing in dense thickets in burnt-out country." No prickly species of *Solanum* is listed for the island. *Solanum simile* belongs to the section *Archaesolanum*, all species of which are unarmed. The section has significantly higher levels of solasodine alkaloids than do the stellate-haired prickly species.

Christensen (1980) reported on the stomach contents of the tammar (*Macropus eugenii*). In a thesis by Kelsall (1965) (not seen) it was stated that tammars browse predominantly on scrub species, particularly *Acacia* but are also attracted to grassy areas. An analysis by Christensen of the stomach contents of four animals disclosed 95, 90, 50% grassy material in three and 95% dicotyledonous material in the fourth. In contrast to *Bettongia*, very little fungal matter was present.

Maynes (1977) studied aspects of the biology of the parma wallaby, *Macropus parma*. This species is native to wet sclerophyll with a thick shrubby understory in association with grassy areas. Although observed to graze in grassy patches, no precise details of their diet were given.

Eight studies of the diet of the large red and grey kangaroos (*Macropus rufus* and *M. robustus*) were located (Chippendale, 1962; Kirkpatrick, 1965; Griffith & Barker, 1966; Chippendale, 1968; Storr, 1968; Bailey et al., 1971; Griffiths et al., 1974; Ellis et al., 1977).

These studies confirm that red kangaroos are essentially grass feeders and that browse is a minor component of their diet and neither can be considered as a major herbivore of *Solanum* although species of the latter occur wherever the larger kangaroos occur. The most prickly species of *Solanum* are not a feature of the plains where the larger grazing kangaroos occur.

Ealey and Main (1967) in a study of the ecology of the euro (*Macropus robustus*) in north-western Australia recorded a fruit of *Solanum lasiophyllum* in the mouth of one euro, but the genus was not otherwise recorded in their diet. However, Dawson and Ellis (1979) when comparing the diet of the euro and *Petrogale xanthopus* showed that though the euro showed a higher percentage of grass at all sampling times the component of plants with stellate trichomes was equally high in July 1974 and February 1978 and low in September 1976. It must therefore be considered as a herbivore of *Solanum*.

Dawson and Ellis (1979) compared the diet of *Petrogale xanthopus* (yellow-footed rock-wallaby) and sympatric herbivores in western New South Wales. The wallaby is now restricted in distribution in New South Wales and South Australia and occurs in rocky ranges. The plants with a tomentum of stellate hairs were classed together and included Solanaceae (*S. petrophilum*), Amaranthaceae, and Malvaceae. After three sampling periods the percentage of particles (plants with stellate trichomes) in the feces of the four animal species was wallaby 6–15%, euro 1–13%, goat 5–23%, rabbit 4–7%. The percentage of samples with stellate hairs was greatest in February 1978, "a notable component."

Copley and Robinson (1982) in their study of the diet of *Petrogale xanthopus* Gray (yellow-footed rock-wallaby) discussed six major dietary components of which one was plants with stellate trichomes (members of the families Solanaceae, Malvaceae, and Amaranthaceae), which could be recognised in the feces because of their characteristic stellate hairs. While this category constituted only about 5% of the diet in winter, it increased to 18–24% in summer (when species of these three plant families would be in active growth), and when fruits of *Solanum* were eaten as well evidenced by the seeds of *Solanum petrophilum* that occur in their feces. All the dietary components occurred in their highest proportion in close association with the rock outcrop. Although Copley and Robinson listed *S. petrophilum* and *S. sturtianum* as the species involved, both were common at the site. *Solanum petrophilum* was eaten throughout the year, in-

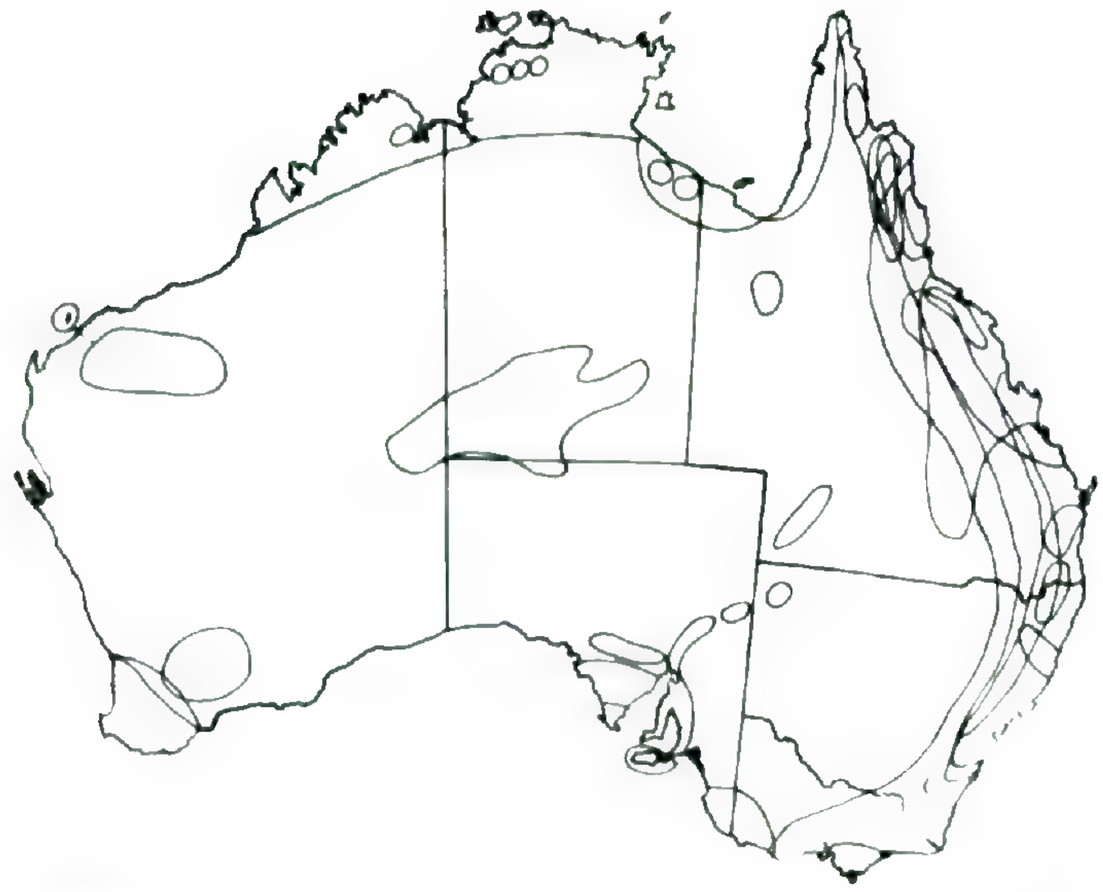

FIGURE 2. Distribution of the known browsing marsupials.

cluding flowers and fruit in spring and summer, and *S. sturtianum* was eaten in the summer.

Hornsby (pers. comm.) has shown me a videotape of a female yellow-footed rock wallaby in the Flinders Ranges eating the stems of *Solanum ellipticum*. The conditions were very dry at the time and the plants desiccated. The hands were used to break up the plant, after which the animal held pieces of the stem in its mouth and appeared to brush them vigorously with its hands to remove or break the prickles off before eating the remainder. The dried leaves did not appear to be eaten. Hornsby also reported then, that at other times of the year the animals selected and ate the flowers of *Solanum*. The bushes were carefully searched and only the flowers were eaten. *Eremophila* flowers were also selectively eaten. In experiments in October to November 1981, the animals were offered wilted and fresh material of *S. ellipticum, S. petrophilum,* and *S. sturtianum*. The flowers and fruits of *S. ellipticum* were eaten. Mature material of *S. sturtianum* was ignored but flowers were eaten. A joey showed distaste on sampling a leaf. The same joey later browsed some of the *S. ellipticum*. It is apparent from these studies that both the yellow-footed rock wallaby and the euro consume *Solanum* spp. and that particularly in summer *Solanum* may compose a measurable portion of their diet.

Short (1980) studied the ecology of the brush-tailed rock wallaby (*Petrogale penicillata*) at Kangaroo Valley (near Nowra) and Goulbourn River (near Muswellbrook) in New South Wales. Here grasses were a dominant element in the diet (33–50%), forbs (28–35%) and shrubs (12–30%) together about equalled the grass. No *Solanum* was listed for the area or recorded in the diet. The intermediate position of *Petrogale* as both a grazer and browser was confirmed.

In a limited study of the swamp wallaby, *Wallabia bicolor,* Edwards and Ealey (1975) concluded that the species was a browser and that although the animals had access to grass and pasture these were scarcely eaten. The animals preferred coarse browse provided by shrubs and bushes. The swamp wallaby occurs in eastern Australia from Cape Yorke to Victoria and though *Solanum* was not mentioned in its diet or its environment, species occur in its area of occurrence. There is evidence that the browsing wallabies do eat prickly *Solanum*. For distribution of browsing marsupials see Figure 2.

Family Phascolarctidae, koala. The koala (*Phascolarctos cinereus*) eats *Eucalyptus* only and is very specialised in its choice of species. It need not be considered in this context as a browsing herbivore.

Family Vombatidae, wombats. The few species are grazers, not browsing herbivores and feed principally on monocotyledons (Wells, pers. comm.).

Family Tarsipedidae, honey possums. Although herbivorous, this species has a specialised diet of pollen, nectar, and fruit and is not a browsing herbivore.

Rodents. Three studies of the diets of Australian rodents (Watts, 1970, 1977; Watts & Braithwaite, 1978) record *Solanum* seed as a minor element of the diet of *Notomys alexis* at Yuendumu (Northern Territory) and there is no other mention of *Solanum*.

P. P. M. Hyland and B. Gray (pers. comm., 1981) stated that rats are known to eat the bark of *S. mauritianum* and *S. torvum*. Both these are alien weedy species that occur in wet tropical areas in eastern Australia. The first is unarmed, the second is prickly. Though possibly significant locally or when in plague numbers there is no evidence to suggest rodents are important as grazers.

THE RESPONSE OF *SOLANUM* IN THE ABSENCE OF HERBIVORES

Hawaii has always been an oceanic island and originally had a very limited vertebrate fauna. The nucleus of the whole flora arrived by long distance dispersal and has since speciated richly. There are about six native species of *Solanum* (St. John, 1973); of these, five are unarmed and

only one, *S. haleakalaense,* is well armed. This last species may have been a late arrival that has not yet lost its prickles or the prickles may deter snails, which are abundant in Hawaii. I have not seen it growing in the field. Carlquist (1970) discussed the prickles on some of the lobelioids in Hawaii. The family Campanulaceae subfamily Lobelioideae is not noted for the development of prickles. The plants are often acrid, bitter, and unpalatable, and many contain indole alkaloids. In Hawaii many species are densely prickly in the young stages and may even have prickly inflorescences and flowers. Carlquist considered this a defense against snails because no other herbivores are well developed in Hawaii. It is possible, although I have no evidence to support it, that the Australian species of *Solanum* with extremely dense stem prickles that grow in the high rainfall sites, such as *S. macoorai, S. oedipus,* and *S. semiarmatum,* may also be protected against snails.

Fiji, without mammalian herbivores, has six species of *Solanum,* probably native, all of which are unarmed, including *S. repandum* Forster, whose close relatives in South East Asia and South America are prickly (Whalen et al., 1981). New Caledonia also lacked mammalian herbivores. Heine (1976) listed 10 native species, of which seven are unarmed and three have traces of prickles. Included in these three is *S. vaccinioides,* which varies from being unarmed to having prickles present, as might be expected if the original immigrant was prickly and the selection pressure for prickles was relaxed.

Tomlinson (1962) discussed the pungency of palms that may develop prickles from leaves, stem emergences, or the roots. He suggested that their role is defence of the single large apical bud and that there are now few large animals capable of tearing open the heart of the palm. Without discussing it further he pointed out that many unarmed palms occur on the isolated islands of the Pacific, where there are few or small vertebrate animals.

These examples support the thesis that prickles are primarily a response to herbivory and have little relationship to the physical environment.

The Effect of Extinct Marsupials

The extinct marsupials, some of which were very large, must have had some effect on the vegetation and in some cases may have acted as seed dispersal agents. Some of these animals survived to the late Pleistocene and certainly overlapped the arrival of aboriginal man in Australia. Sanson (1978) considered most of the extinct macropodids to be browsers. Many of the others were herbivores, e.g., diprotodontids, phascolarctids, palorchestids, and vombatids, and included both browsers and grazers (Archer, 1981). Janzen (1982) claimed to detect a suite of Central American plants whose fruits were probably dispersed by the recently extinct large herbivores of that area. A parallel in Australia is not immediately obvious, but the influence of the browsers on some of the remaining vegetation, particularly in those areas now occupied by the grazing kangaroos, might be worth searching for.

Conclusion

The evidence assembled suggests that prickles on *Solanum* are not an adaptation to aridity. The scattered and incomplete records of the diet of Australian vertebrate herbivores suggests that the relic group of marsupials called wallabies and prickly *Solanum* do in general coincide. The distribution of wallabies may have contracted in geologically recent times due to increasing aridity but prickly *Solanum* still remain in some areas where wallabies are now extinct.

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ZAPOTECA: A NEW GENUS OF NEOTROPICAL MIMOSOIDEAE[1]

HÉCTOR M. HERNÁNDEZ[2]

ABSTRACT

The existence of consistent variation patterns in polyad characteristics, seedling morphology, chromosome numbers, and several reproductive features within the American species of *Calliandra* Benth. has revealed the presence of two well defined taxonomic units, the first one including the species of ser. *Laetevirentes,* and the second the remaining neotropical species. The lack of intermediate forms between the two units suggests that *Calliandra,* as originally conceived by Bentham, is polyphyletic. Therefore, the creation of the genus *Zapoteca,* consisting of ca. 25 taxa distributed from southwestern United States and northern Mexico to northern Argentina, is proposed to include the species of ser. *Laetevirentes.* New combinations are presented for *C. caracasana, C. formosa, C. lambertiana, C. media, C. mollis, C. portoricensis,* and *C. tetragona.*

RESUMEN

La existencia de patrones estables de variación en las características de las poliades, morfología de las plántulas, números cromosómicos, así como en varios rasgos reproductivos en especies americanas de *Calliandra* Benth. ha revelado la presencia de dos unidades taxonómicas bien definidas. La primera de éstas incluye a las especies de la ser. *Laetevirentes,* y la segunda al resto de las especies neotropicales. La ausencia de formas intermedias entre las dos unidades sugiere que el género *Calliandra,* como fué concebido originalmente por su autor, es polifilético. En consecuencia, se propone la creación del género *Zapoteca* para incluir a los miembros de la ser. *Laetevirentes.* El género está constituido por aproximadamentre 25 taxa distribuidos desde el suroeste de los Estados Unidos y el norte de México hasta el norte de Argentina, con un claro centro de diversificación en el sur de México. Se presentan también nuevas combinaciones para *C. caracasana, C. formosa, C. lambertiana, C. media, C. mollis, C. portoricensis* y *C. tetragona.*

This paper reports part of a biosystematic study of the genus *Calliandra* (Leguminosae: Mimosoideae, tribe Ingeae). As currently circumscribed, this genus includes a relatively heterogeneous assemblage of about 150 species native predominantly in tropical and sub-tropical regions in the Americas. In addition, a few species are found in continental Africa (Thulin et al., 1981), Madagascar, and India (Paul, 1979). The genus was originally described by G. Bentham in 1840, who subsequently (1844), and more formally in his monograph of the Mimosoideae (1875), subdivided it into five series based on leaf and inflorescence characteristics: ser. *Macrophyllae, Laetevirentes, Pedicellatae, Nitidae,* and *Racemosae.* Since then, many new species have been described, and the genus has been included in a number of floras; nevertheless, Bentham's original concept of the genus remains unchanged.

Palynological studies have contributed substantially to the understanding of the infrageneric relationships in *Calliandra* (Guinet, 1965, 1969, 1981; Guinet & Barth, 1969; Sorsa, 1969; Niezgoda et al., 1983). The New World species may be classified into two basic pollen groups, according to their contrasting polyad features. The first group (Type IB in Guinet, 1965) includes all the species of ser. *Laetevirentes,* and two species placed by Bentham into ser. *Macrophyllae.* Polyads in this group are 16-grained, radially symmetrical, acalymmate, with granular ektexine structure. These polyad characteristics are found in all the other genera of the tribe Ingeae; however, species in this portion of *Calliandra* have

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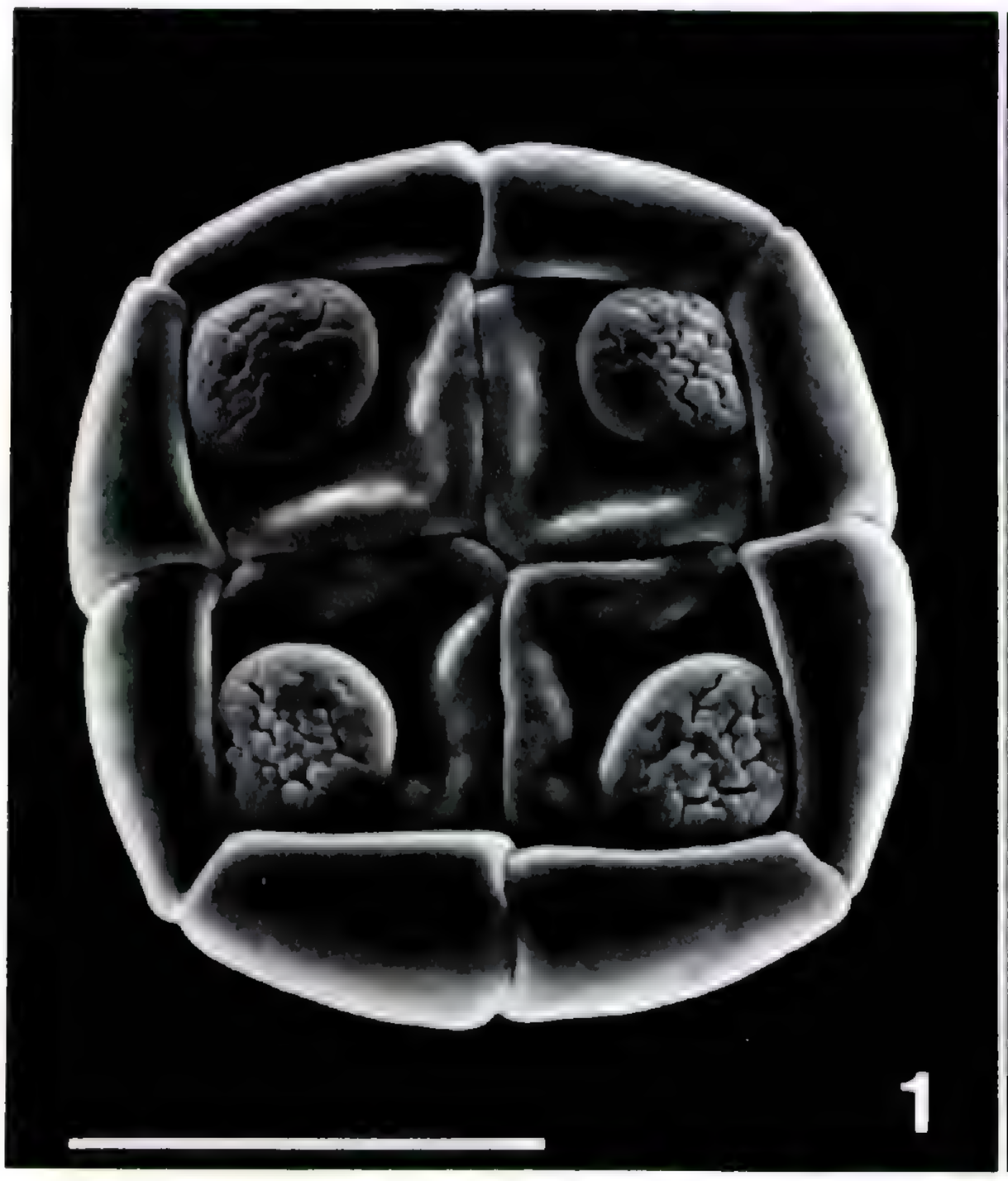
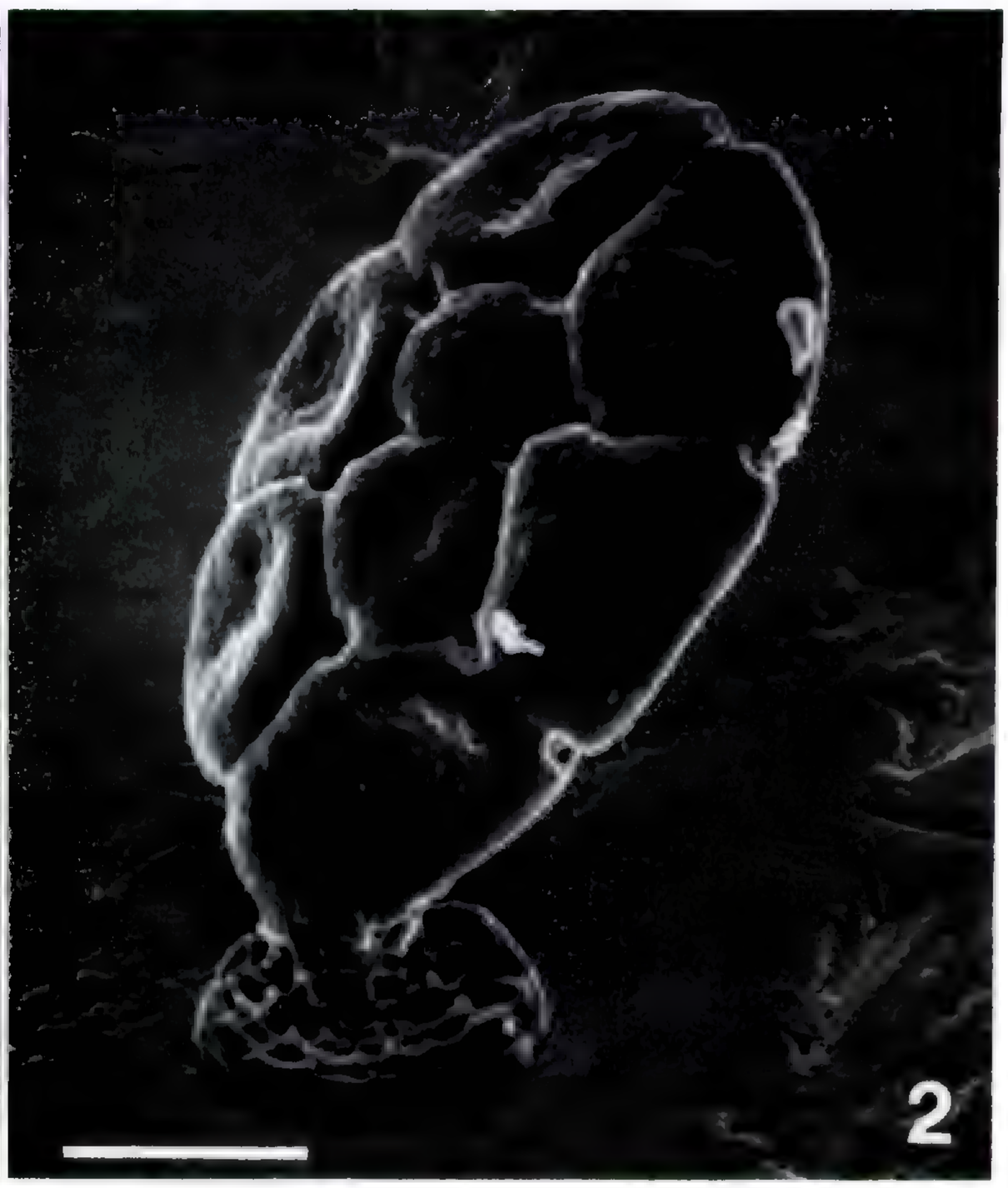




FIGURES 1, 2. Polyad types of *Zapoteca* and *Calliandra*.—1. Unacetolysed 16-grained polyad of *Z. tetragona* (cult. at MO from: Mexico, Veracruz, *Johnson 1582*).—2. Unacetolysed 8-grained polyad of *C. houstoniana*. The sticky appendage on the basal cell is attached to the SEM stub (cult. at MO from: Mexico, Chiapas, *Johnson 363-78*). Scales = 50 μm.

very distinctive circular thickenings in the central cells generally on one side of the polyad (Fig. 1), which are an excellent diagnostic character. The remaining species of the genus, in contrast, have specialized 8-grained, bisymmetric, calymmate polyads, with columellar/granular exine structure. In addition, the 8-grained polyads have a mucilaginous structure on the "basal" cell (on the narrow part of the polyad), which is associated with transfer by pollinators (Fig. 2). The nature of polyad cohesion (calymmate), the characteristics of the ektexine, and the presence of the sticky appendage in the "basal" cell of the 8-grained polyads in *Calliandra*, form a combination of features found nowhere else in the Mimosoideae. It is important to mention that no intermediate forms have been found between the two pollen groups (Ph. Guinet, pers. comm.).

The outstanding differences between the 16- and 8-celled polyads have provided evidence to suggest that the genus should be subdivided (Guinet, 1969). Moreover, Niezgoda et al. (1981) have suggested a separate generic or even tribal status for the species of *Calliandra* with 8-celled polyads, in light of their great distinctiveness in the whole subfamily.

On the basis of this evidence, several studies were initiated in order to test the general validity of this relationship within *Calliandra*. These studies, the results of which will be outlined below, include surveys on seedling morphology, reproductive biology, and chromosome numbers of species throughout the genus. Although these investigations are still in progress, they show the same variation pattern found in the palynological work. The dichotomy resulting from the analysis of these characters acquires a special meaning when it is considered that the identity of *Calliandra* has been traditionally based on the presence of a single morphological feature: the elastically dehiscent pods. All other evidence indicates that ser. *Laetevirentes* and the rest of *Calliandra* species do not constitute a monophyletic assemblage and suggests that these taxonomic units must be placed into separate genera.

The genus name *Calliandra* Benth. has been conserved over *Anneslia* R. A. Salisbury (Int. Code Bot. Nomencl. p. 267, no. 3444. 1961), with *C. houstonii* (L'Hér.) Benth., nom. illeg. [*Gleditsia inermis* L., *C. inermis* (L.) Druce] as the type species. Bunting (Taxon 16: 469–472. 1967) has proposed amending the conservation

of *Calliandra* with *C. grandiflora* (L'Hér.) Benth. as the type species, because of the difficulty of typifying *C. inermis*; however, this proposal was rejected (Taxon 17: 466. 1968). Bentham (1875) considered *C. houstonii* as belonging to his ser. *Racemosae*. Similarly, the synonyms of *Calliandra, Clelia ornata* Casar. [= *Calliandra harrissii* (Lindley) Benth.], and *Codonandra purpurea* Karsten. [= *Calliandra codonandra* (Karsten.) Benth.] were included in sers. *Macrophyllae* and *Nitidae* respectively. Consequently, as no published generic name seems to be available for any member of ser. *Laetevirentes*, the following new name is proposed.

Zapoteca H. Hernández, gen. nov. (Leguminosae–Mimosoideae, trib. Ingeae). TYPE: *Z. tetragona* (Willd.) H. Hernández, comb. nov. *Acacia tetragona* Willd. Species Plantarum 4(2): 1069. 1806. Venezuela, Caracas, in ripis arenosis fluvii Guairito, *Bredemayer 17* [lectotype: B (Herbar Willdenow no. 19147) here designated; phototypes MO!, MEXU!].

Calliandra Benth. ser. *Laetevirentes* Benth. Hook. J. Bot. 3: 97. 1844.

Frutices ramosi, erecti vel scandentes, inermes, ramis teretibus vel tetragonis. Stipulae saepe conspicuae, foliaceae, persistentes. Folia bipinnata, foliolis saepe membranaceis vel interdum coriaceis. Inflorescentia capitata, pedunculata, axillaris vel in pseudopanicula, homomorpha, heterogama vel homogama, bracteata. Flores sessiles, actinomorphi, 5-meri vel rarius 6-meri. Calyx cupulatus, dentatus, glaber vel pubescens. Corolla infundibuliformis vel campanulata, petalis revolutis. Stamina numerosa (ca. 30–60); filamentis longe exsertis, 19–43 mm longis, albis, roseis vel purpureis; staminum tubo incluso; antheris eglandulosis. Pollinia 16-cellularia, discoidea, heteromorpha; cellulis centralibus papillatis. Ovarium breviter stipitatum, 10–15 ovulatum; stylo filiformi, 18–45 mm longo; stigmate apicali, cupulato. Legumen membranaceum ad coriaceum, siccum, lineare, rectum, plano-compressum, margine incrassato, valvis ab apice ad basin elastice dehiscentibus. Semina indurata, exarillata. $x = 13$.

Shrubs ramose, erect or scandent, unarmed, glabrous or pubescent, with the young branches terete or 4-angled. Phyllotaxy distichous. Stipules usually conspicuous, leafy, usually persistent in mature leaves. Leaves bipinnate; petiole rarely with nectariferous glands; leaflets opposite, sessile, usually membranous or rarely coriaceous, usually glaucous underneath, glabrous or pubescent. Inflorescences axillary and/or pseudopaniculate, pedunculate, capitate, densely flowered, homomorphic, heterogamic or homogamic, bracteate. Flowers sessile, actinomorphic, 5- rarely 6-merous; calyx cup-shaped, dentate, glabrous or pubescent; corolla campanulate or infundibuliform, membranous, with the petals revolute, valvate in bud; nectariferous disk present in all flowers; stamens numerous (ca. 30–60), filaments long-exserted, ca. 19–43 mm long, white, pink, or purple, staminal tube inserted; anthers dithecal, dorsifixed, eglandular, every anther containing eight polyads; polyads 16-grained, discoid, heteromorphic, with eccentric lens-shaped thickenings on central cells; ovary 1, shortly stipitate, with ca. 10–15 ovules; style filiform, ca. 15–56 mm long in fertile pistils; stigma apical, cup-shaped. Legume dry, membranaceous to coriaceous, linear, straight, plano-compressed, with the margins thickened, usually with constrictions in interseminal areas, valves dehiscing elastically from the apex to the base. Seeds in one series, hard, ovate to rhomboid, non-arillate, non-alate usually with irregular or regular 90 percent pleurogram. Seedlings phaneroepigeal, with the cotyledons ephemeral, foliaceous, sessile, elliptic to elliptic-ovate; the first and second eophylls opposite, the third and fourth alternate; leaflets usually membranous. $x = 13$.

Z. caracasana (Jacq.) H. Hernández, comb. nov. *Mimosa caracasana* Jacq., Collectanea 4: 142. 1791. Fig. Jacq., Icon. pl. rar. 3: 20, t.632. 1793.

Z. formosa (Kunth) H. Hernández, comb. nov. *Acacia formosa* Kunth, Mim. p. 102, t. 32. 1822.

Z. lambertiana (G. Don) H. Hernández, comb. nov. *Acacia lambertiana* G. Don, Edwards Bot. Reg. 9: t. 721. 1823. TYPE: México, locality unknown; cultivated by G. Don, from material sent to him by Mr. Lambert from Boyton, where plants of this species had been raised from seeds collected in México (lectotype, K!, here designated).

Z. media (M. Martens & Galeotti) H. Hernández, comb. nov. *Acacia media* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10: 316. 1843. TYPE: México, Hidalgo, Hacienda de Guadalupe près Mextitlán *Galeotti 3362* pro parte (lectotype, BR!, here designated).

Z. mollis (Standley) H. Hernández, comb. nov. *Calliandra mollis* Standley, Contr. U.S. Natl. Herb. 17: 431. 1914. TYPE: Costa Rica, Puntarenas, near Nicoya, *Tonduz 13536* [holotype, US! (sheet no. 578114); isotypes, BM!, F!, G!, GH!, K!, NY!, US!].

Z. portoricensis (Jacq.) H. Hernández, comb. nov.
Mimosa portoricensis Jacq., Collectanea 4: 143. 1791. Fig. Jacq., Icon. pl. rar. 3: 20, t. 633. 1793.

This genus is named to pay homage to the Zapotec people, who since 500 B.C. (Flannery & Marcus, 1983) to the present have inhabited the varied lands of Oaxaca, Mexico, the center of diversity of this group of plants.

Zapoteca is a rather homogeneous assemblage morphologically, consisting of about 25 taxonomically difficult taxa, distributed from northern Mexico and southwestern United States to northern Argentina, ranging from sea level to ca. 2,150 m. The greatest concentration of species is in southern Mexico, especially in the state of Oaxaca. Natural populations occur primarily in disturbed habitats derived from a variety of vegetation types, from semi-arid scrub to relatively wet forests; however, the greatest diversification has occurred in tropical dry forests. Several species have very wide ranges (e.g., *Z. formosa, Z. portoricensis, Z. tetragona*) and evidently have outstanding ability to colonize new habitats. Other species are narrow endemics (e.g., *Z. mollis*).

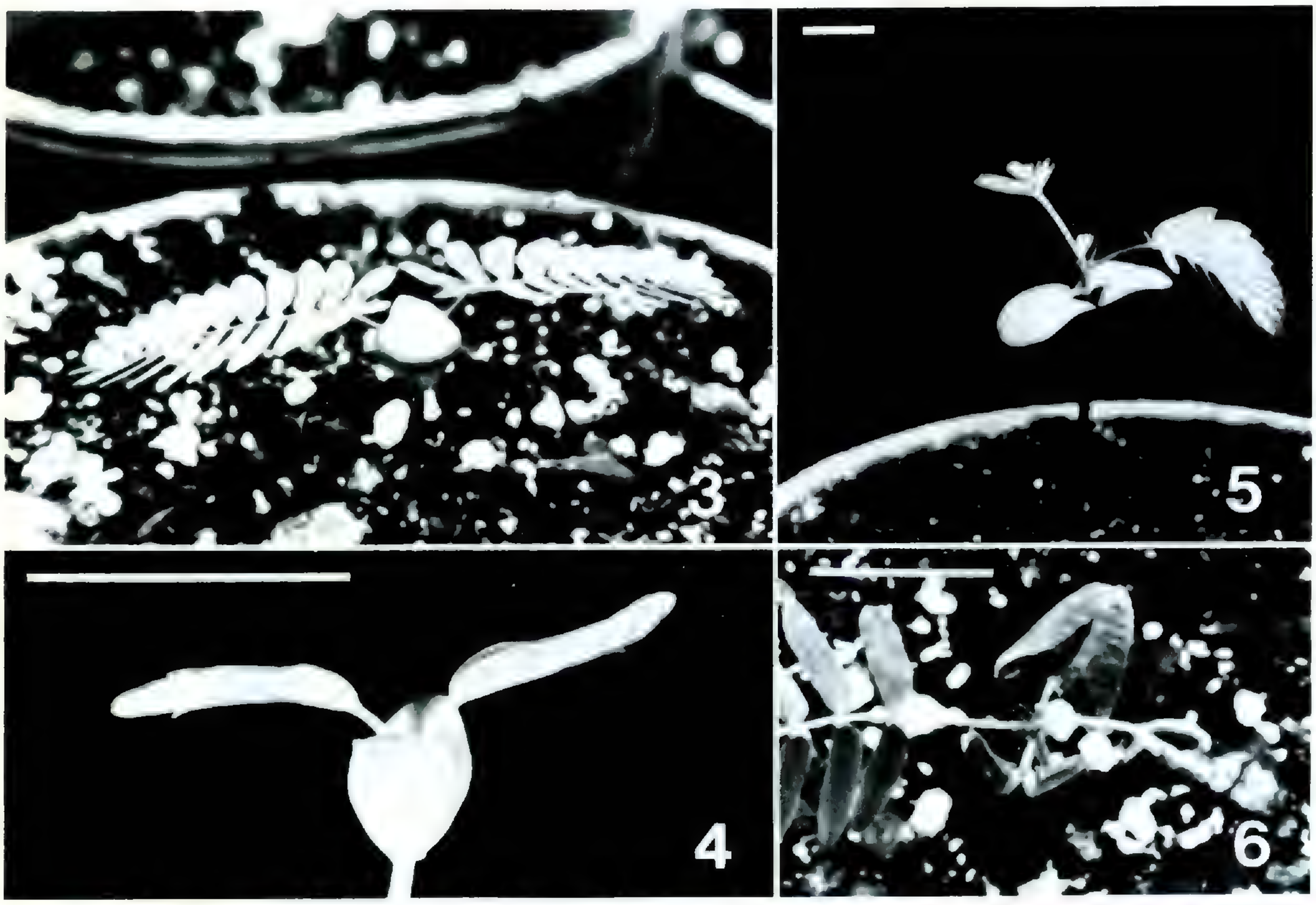
The totality of published specific epithets (45) included within *Calliandra*, ser. *Laetevirentes* is clearly comprised in *Zapoteca*. As mentioned above, 25 taxa are currently recognized in the genus, and new combinations are proposed here for seven of them. The remaining ones will be treated in a future revision, due to the fact that their taxonomic status—whether species or subspecies—is still unclear. Because the species of *Zapoteca* are quite uniform morphologically, the genus is easy to identify. There are, however, some *Calliandra* species, not members of ser. *Laetevirentes*, that must also be taken into consideration because they have some features typical of *Zapoteca*. These are *C. amazonica* Benth. and *C. aculeata* Spruce ex Benth., both placed by Bentham (1875) in his ser. *Macrophyllae*, who, however, had previously noted similarity between the structure of the inflorescence of *C. amazonica* and that of *Z. portoricensis* (Bentham, 1844). Subsequently, Guinet (1965) found that the polyad characteristics of these two species are essentially the same as those of Bentham's ser. *Laetevirentes*. The small number and larger size of the leaflets in *C. amazonica* and *C. aculeata*, and the presence of stipular spines in *C. aculeata*, are the main characters differentiating them from the species of *Zapoteca*. In the light of present evidence, it seems clear that these two species do not fit within the limits of *Calliandra* as proposed in this paper; however, their inclusion within *Zapoteca* or another genus needs further study.

DESCRIPTION OF SOME CRITICAL CHARACTERS IN *ZAPOTECA* AND *CALLIANDRA*

This section provides the supporting evidence that reflects the heterogeneous nature of *Calliandra* as structured by G. Bentham. The characters analyzed are described concisely; comprehensive accounts will be provided in a subsequent paper.

Seedling morphology. A total of 95 seedling samples have been studied, representing nine species of *Zapoteca* and 31 of *Calliandra*. In describing the seedlings I have selected four main characters: 1) degree of persistence of cotyledons, 2) morphology of cotyledons, 3) type of succession of eophylls, and 4) number of leaflets. Of these, cotyledon features revealed the most striking contrast between the *Zapoteca* seedlings and those of *Calliandra*. All the species of *Zapoteca* have seedlings with elliptic or elliptic-ovate, sessile, foliaceous, and ephemeral cotyledons (Figs. 3, 4). In contrast, *Calliandra* seedlings have sagittate, petiolate, fleshy, and relatively persistent cotyledons as common characters (Figs. 5, 6). While the type of succession of the eophylls and the leaflet characteristics were remarkably constant in the *Zapoteca* seedlings, these characters display a high degree of variation in *Calliandra*. This variation allows a further grouping into five subtypes, which correspond to a certain extent with Bentham's series. In sum, the morphological characteristics in the seedlings of *Zapoteca*, which are notably homogeneous, differ from those of *Calliandra* primarily in the basic features of the cotyledons. The absence of intermediate seedling forms between *Zapoteca* and *Calliandra* reflects the lack of close relationships between the two genera.

Reproductive biology. The species of *Zapoteca* differ from those of *Calliandra* in a number of aspects of their reproductive behavior. In *Zapoteca* the individual flowers are always arranged in compact, homomorphic, spherical inflorescences (Fig. 7). In *Calliandra*, in contrast, there are more diverse patterns of inflorescence organization. The basic type seems to be the axillary, obconiform inflorescence (Fig. 8) from which other types have been derived. The racemose



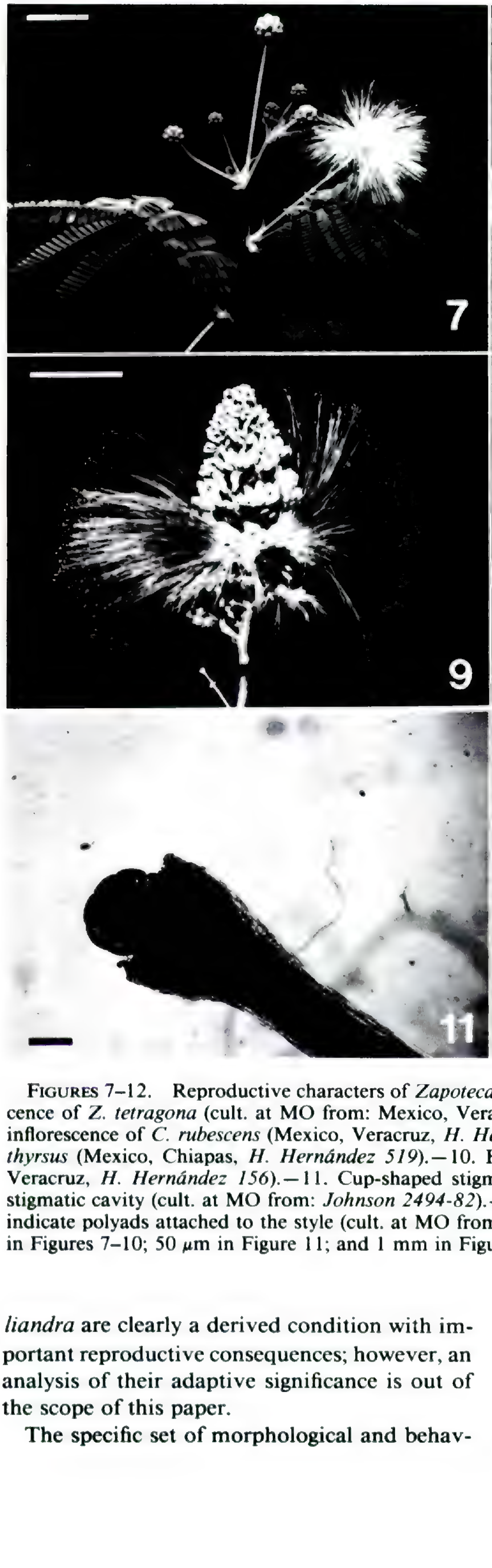
FIGURES 3–6. Seedling types of *Zapoteca* and *Calliandra*.—3. *Z.* sp. nov. (cult. at MO from: Mexico, Oaxaca, *Torres 4167*).—4. *Z. tetragona* (cult. at MO from: Mexico, Veracruz, *H. Hernández 167*).—5. *C. calothyrsus* (cult. at MO from: Panama, David, *Johnson 929-79*).—6. *C. eriophylla* (cult. at MO from: Mexico, Oaxaca, *Torres 4192*). Scales = 10 mm.

inflorescences of the species of ser. *Racemosae* (Fig. 9), a group basically endemic to Mexico and Central America, represent the type that has departed most from the ancestral type of inflorescence.

An interesting reproductive feature found in most species of *Calliandra* ser. *Nitidae, Macrophyllae,* and in some of the *Pedicellatae* is the presence of heteromorphic inflorescences (Fig. 10). In general, these have one to several central flowers whose morphology is modified in relation to the peripheral ones. The central flowers are the only ones bearing nectaries; these are larger and have the staminal tube well exserted from the corolla apex. This floral specialization, which is also found in other genera of the tribe Ingeae (e.g., *Albizia*), has important consequences on the foraging behavior of flower visitors. Because the central flowers are more conspicuous and provide nectar rewards, the visitors forage actively on them, seeking them out and therefore increasing the possibilities of pollinating a higher number of hermaphroditic flowers in the inflorescence in the course of a single visit.

A detailed analysis of sex expression carried out on flower material collected in natural populations has shown that andromonoecy, expressed morphologically by gynoecium abortion, is widespread in both genera. In contrast to the opinion of Nevling and Elias (1970), this study has shown that variation in the presence of andromonoecy is not consistent with the variation patterns found in other characters (e.g., polyads, seedlings, chromosome numbers).

Another reproductive feature characteristic of *Zapoteca* species is the stigma type. All the species in this genus have delicate, cup-shaped stigmas, with a very narrow area of receptivity that can hold just a single 16-celled polyad (Fig. 11). As far as it has been possible to observe, this stigma type is found in all the genera of the tribe Ingeae, except *Calliandra* (see for example, Koptur, 1983; Hoc, 1981), and in 17 genera of the Mimosoideae (Lewis, pers. comm. via Polhill; see also Simpson et al., 1977; Nevling & Niezgoda, 1978; Kenrick & Knox, 1981; Lewis & Elias, 1981; Hopkins, 1984). In contrast, the species of *Calliandra* have very distinctive expanded, fungiform, discoid, or capitate stigmas with a much wider area of polyad receptivity (Fig. 12). The stigma types in *Cal-*



FIGURES 7–12. Reproductive characters of *Zapoteca* and *Calliandra*.—7. Spherical, homomorphic inflorescence of *Z. tetragona* (cult. at MO from: Mexico, Veracruz, *Johnson 1582*).—8. Obconiform, heteromorphic inflorescence of *C. rubescens* (Mexico, Veracruz, *H. Hernández 156*).—9. Racemose inflorescence of *C. calothyrsus* (Mexico, Chiapas, *H. Hernández 519*).—10. Heteromorphic inflorescence of *C. rubescens* (Mexico, Veracruz, *H. Hernández 156*).—11. Cup-shaped stigma of *Z. caracasana* with a 16-grained polyad in the stigmatic cavity (cult. at MO from: *Johnson 2494-82*).—12. Fungiform stigma of *C. houstoniana*. The arrows indicate polyads attached to the style (cult. at MO from: Mexico, Chiapas, *Johnson 363-78*). Scales = 40 mm in Figures 7–10; 50 μm in Figure 11; and 1 mm in Figure 12.

liandra are clearly a derived condition with important reproductive consequences; however, an analysis of their adaptive significance is out of the scope of this paper.

The specific set of morphological and behavioral reproductive characteristics in *Zapoteca* and *Calliandra* is associated with particular classes of pollinators. Field and greenhouse observations, in conjunction with some literature reports, have allowed us to characterize these

TABLE 1. Chromosome numbers in *Zapoteca* and *Calliandra*. The asterisk (*) indicates first report for the species.

Species	Chromosome Number *n*	Chromosome Number 2*n*	Reference
*Zapoteca tetragona**		26	México, Veracruz, Mun. Catemaco, a 1 km de Sontecomapan por camino a Coxcoapan, *H. Hernández 167* (MO, MEXU)
		26	México, Veracruz, Mun. Córdoba, sobre la autopista Fortín-Córdoba, *H. Hernández 827* (MO, MEXU)
		26	Costa Rica, Cartago, Finca Perla, entre Reserva de Vida Silvestre Tapantí y Purisil, *H. Hernández 675* (MO, MEXU)
*Z. portoricensis**		26	México, Veracruz, 6.8 km N de Xalapa por camino a Naolinco, *H. Hernández 154* (MO, MEXU)
*Z. formosa**		26	México, Oaxaca, Dist. Tehuantepec, 11.1 km SW del entronque carr. Tehuantepec-Oaxaca, por camino a Buenos Aires, *R. Torres 4262* (MO, MEXU)
		26	México, Yucatán, 20 km S of Progreso, *D. Johnson 483-78* (MO)
*Z. media**		26	México, Hidalgo, Mun. Metztitlán, Paso del León, Barranca de Venados, *A. Delgado 53* (MEXU)
Z. sp. nov. (1)*		26	México, Oaxaca, Dist. Mixe, 6 km N de Mitla por camino a Totontepec, *R. Torres 3947* (MO, MEXU)
Z. sp. nov. (2)*		26	México, Oaxaca, Dist. Tehuantepec, El Manguito, SW de El Limón, *R. Torres 4167* (MO, MEXU)
Ser. Nitidae			
Calliandra surinamensis		16	Atchinson (1949)[1]; Goldblatt (1981b)
C. surinamensis	8		Bir et al. (1980)
C. magdalenae		16	Goldblatt (1981b)
C. haematocephala		16	Atchinson (1951)
C. tweedyi		16	Bir and Kumari (1978, 1979)
C. pittieri		32	Shibata (1962)
Ser. Macrophyllae			
*C. tergemina**		16	México, Jalisco, Mun. la Huerta, Estación de Biología Chamela, *E. Lott 1686* (MO, MEXU)
Ser. Racemosae			
C. houstoniana	8		Bir et al. (1980)
C. calothyrsus		22	Goldblatt (1981b)[2]
*C. rusbyi**		22	México, Guerrero, Mun. Coyuca, Torre de Microndas, 5 km NW de El Zapote, por carr. Atoyac-Cayuca, *H. Hernández 865* (MO, MEXU)
C. sp. nov.*		22	México, Oaxaca, Dist. Putla. 11.5 km NE de Putla por carr. a Tlaxiaco, *H. Hernández 465* (MO, MEXU)

[1] Referred to as *C. haematocephala*.
[2] Referred to as *C. confusa*.

genera in terms of their pollination mechanisms. The pollination of species of *Zapoteca* appears to be exclusively nocturnal, and a number of settling moth species (families Noctuidae, Pyralidae, and Geometridae, etc.) consistently have been observed foraging on inflorescences of *Z. portoricensis*, *Z. formosa*, *Z. media*, and *Z. tetragona* (pers. obs.). *Calliandra*, however, is more diverse in its pollination systems. Several species of the genus have been reported as hawkmoth-pollinated (Cruden et al., 1976; Haber & Frankie, 1984; pers. obs.), whereas others are hummingbird pollinated (Snow & Snow, 1972; Arroyo, 1981; pers. obs.). Interestingly, as was noted by

TABLE 2. Comparative characters of *Zapoteca* and *Calliandra*.

	Zapoteca	*Calliandra*
Leaflets	thin membranaceous, rarely coriaceous	chartaceous to coriaceous
Inflorescence	spherical heads; homomorphic	obconiform, racemose, rarely spherical; homomorphic or heteromorphic
Polyads	16-grained, discoid	8-grained, bisymmetric, with viscid appendage in "basal" grain
Stigmas	cup-shaped, with narrow area of polyad receptivity	expanded; fungiform, discoid, or capitate
Legume	membranaceous to coriaceous	more rigid; coriaceous, ligneous, rarely membranaceous
Seedlings	cotyledons ovate, sessile, foliaceous, ephemeral	cotyledons saggitate, petiolate, fleshy, persistent
Chromosome numbers	$x = 13$	$n = 8, 11$

Arroyo (1981) for other genera of the Mimosoideae, the limits between sphingophily and ornithophily are not well established in a number of species of *Calliandra* [e.g., *C. magdalenae* (Bertero ex DC.) Benth., *C. grandiflora* (L'Hér.) Benth., *C. houstoniana* (Miller) Standley]. In these species the filaments are red or a combination of white and red, and the flowers remain in anthesis during the night and the first hours of the day, allowing a succession of sphingid moth and hummingbird visits. The relative effectiveness of each pollinator class will be analysed elsewhere. A similar situation is probably found in *C. calothyrsus* Meissn. (= *C. confusa* Sprague & Riley, and *C. similis* Sprague & Riley), whose flowers have been reported to be visited by honeycreepers (Coerebidae; Skutch, 1981), bats (Holdridge & Poveda, 1975), and sphingid moths (pers. obs.). Visitors of high energetic requirements often seek such flowers with their copious nectar product if the nectar is relatively accessible.

Cytogenetics. Although *Calliandra* sensu Bentham is a large genus, very little information on its chromosome numbers has been published (Table 1). The counts I have obtained so far in the hitherto cytologically unknown *Zapoteca* are $n = 13$ (Table 1), which is consistent with the basic chromosome numbers reported for all the genera of the Ingeae ($x = 13$; Goldblatt, 1981a). *Calliandra* sensu stricto, in contrast, represents the only known exception to $x = 13$, with several species distributed in sers. *Nitidae, Macrophyllae,* and *Racemosae* having $n = 8$ (Table 1). Furthermore, *C. calothyrsus* (Goldblatt, 1981b) and other members of ser. *Racemosae* are known to be $n = 11$, and *C. pittieri* is polyploid, $n = 16$ (Shibata, 1962). Table 2 shows a summary of the basic characters of *Zapoteca* and *Calliandra*.

GENERAL REMARKS

The segregation of the species of *Calliandra* ser. *Laetevirentes* into the genus *Zapoteca* as proposed in this paper constitutes the first step toward a comprehensive study of *Calliandra* (Forero, 1984; Hernández, 1984; Romeo, 1984). The *Calliandra* species from Madagascar and India must be studied critically in the same way as the *Zapoteca* species because these are palynologically dissimilar to the remaining species (Guinet, 1965). The neotropical species of *Calliandra* as circumscribed here, however, are certainly monophyletic. We must pursue an integral infrageneric classification of this genus in order to improve Bentham's taxonomic framework. Several taxa, primarily South American, do not fit into this classification, and evidence indicates that sers. *Macrophyllae* and *Pedicellatae* are artificial.

The presence of two species of *Calliandra* in restricted areas of eastern Africa provides an interesting phytogeographic pattern. These species, which are clearly related to the neotropical ones (Thulin et al., 1981), probably represent remnants of more diversified taxa that existed in Africa before the widespread extinction that has taken place in this continent since the close of the Oligocene (Raven & Axelrod, 1974). The polyad characteristics of these species are basically the same as those of the neotropical *Calliandra* (Thulin et al., 1981) with the exception that the cells are free from one another (acalym-

mate). The existence of this feature is a further indication of the primitive nature of these species.

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DISTRIBUTION OF NONPROTEIN IMINO AND SULPHUR AMINO ACIDS IN *ZAPOTECA*[1]

JOHN T. ROMEO[2]

ABSTRACT

Seeds of eight and leaves of nine species of *Zapoteca* were surveyed for nonprotein sulphur-containing amino acids and nonprotein imino acids, and the patterns compared with those of *Calliandra* species. S-(β-carboxyethyl)-cysteine, the major free seed amino acid in all *Calliandra* species examined, and S-(β-carboxyisopropyl)-cysteine, a lesser constituent, were not detected in *Zapoteca* species. Conversely, an uncharacterized compound not significantly present in *Calliandra* is the major free amino acid of *Zapoteca*. The major imino acids of *Zapoteca*, trans-trans-4,5-dihydroxypipecolic acid, trans-4-hydroxypipecolic acid, and cis-5-hydroxypipecolic acid, are a consistent feature of the genus, but these same compounds are also found together in many *Calliandra* species. The chemical data are interpreted as supportive evidence for the distinctiveness of these two closely allied groups of plants.

Calliandra (Mimosoideae) is a large heterogeneous group of tropical-subtropical woody shrubs and trees found mainly in the Americas, extending from the southern U.S. to Argentina. About 200 species have been described. *Zapoteca*, a new genus (Hernández, 1986) consists of a morphologically homogeneous group of 25 taxa distributed largely in southern Mexico. The group includes all plants placed previously under Bentham's series *Laetevirentes* of *Calliandra* (1875).

Species of both genera are characterized by large amounts of rare unusual imino acids that accumulate in both seeds and leaves. Nine compounds, derivatives of pipecolic acid, previously have been isolated from various *Calliandra* species (Marlier et al., 1972, 1979; Bleecker & Romeo, 1981, 1983; Romeo et al., 1983). They include four monohydroxylated pipecolic acids (trans-4-, trans-5-, cis-4-, and cis-5-hydroxypipecolic acids); four dihydroxylated pipecolic acids (trans-cis-, trans-trans-, cis-trans-, and cis-cis-4,5-dihydroxypipecolic acids); and trans-4-acetylaminopipecolic acid. The last two compounds are known only from *Calliandra*. Populational sampling of a number of species has established that there is essentially no intraspecific variability in the rare compounds (Romeo, 1984). Complementary laboratory experiments have shown that the compounds are stable under various conditions of imposed water and UV stress (Bleecker & Romeo, in prep.; Balis & Romeo, unpubl. data). The rarity of the compounds coupled to their apparent ecological stability indicates that they are suitable for use in taxonomic studies. Analysis of *Calliandra* leaf material of over 100 species has produced several different chemical patterns (Romeo, 1984 and unpubl. data). The usefulness of these chemical groups in helping to establish a natural grouping of species within the large genus *Calliandra*, however, is yet to be determined. *Calliandra* is currently undergoing systematic revision, and the chemical findings will be interpreted in conjunction with results emerging from other fronts (see below).

The seeds of *Calliandra* are characterized additionally by large amounts of nonprotein sulphur-containing amino acids. S-(β-carboxyethyl)-cysteine (S-CEC) is the major compound. It is rapidly metabolized upon germination and is absent from mature foliage, but continues to appear in new emerging leaves up to 70 days after germination (Swain & Romeo, 1986). Lesser amounts of other related S-containing amino acids are also present in seeds. S-(β-carboxyisopropyl)-cysteine (S-CIC), djenkolic acid, and acetyldjenkolic acid are found frequently along with uncharacterized oxidized derivatives of these compounds (Krauss & Reinbothe, 1970; Romeo & Swain, unpubl.).

The presence of these two classes of unusual amino acids in *Calliandra* has led to a large-scale study of the distribution of these compounds in leaves and seeds. *Calliandra*, which has received little significant taxonomic treatment since the monograph by Bentham (1875), is now the focus

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ANN. MISSOURI BOT. GARD. 73: 764–767. 1986.

of much research (Forero, 1984). In addition to morphological studies, which have been initiated by Forero (Colombian species), Ataide (Brazilian species), and Hernández (Central American-Mexican species), developmental, palynological, chromosomal, and chemical studies are underway. The work described herein is part of this multidisciplinary project. With the establishment of a new genus *Zapoteca* (Hernández, 1986) to include several species previously considered under *Calliandra,* it is an appropriate time to put forth some of the data that are emerging from the chemical studies. The purpose of this paper is to present chemical data on *Zapoteca* species, and to discuss the significance of these findings particularly in relation to *Calliandra.*

Materials and Methods

Collection of Material. Species are listed with voucher data in Tables 1 and 2.

Extraction and chromatographic methods. One hundred mg of material were ground and extracted by the method described in Romeo et al. (1983). A MeOH-$CHCl_3$-H_2O (12 :5 : 1) extract was separated into an upper aqueous and lower $CHCl_3$ layer by addition of H_2O and $CHCl_3$. The aqueous phase was removed, evaporated to dryness and redissolved in 25% EtOH. This was used for paper chromatography and high voltage paper electrophoresis. Samples for quantitative analysis on the amino acid analyzer (Dionex D-300) were prepared by evaporating aliquots of the above solution and redissolving them in 0.2 M Na^+ buffer (Dionex Femto buffer 1A, pH 2.0). Chromatographic solvents used were 1) BuOH-HOAc-H_2O (12:3:5), 2) 80% PhOH-H_2O (w/v) in the presence of NH_3 vapor, 3) BuOH-HCO_2H-H_2O (15:3:2). High voltage electrophoresis was performed on paper in buffer (pH 1.9).

Identification of compounds. Compounds were identified from R_f values and ionic mobilities (Seneviratne & Fowden, 1968; Romeo et al., 1983), comparison with authentic standards, and color reactions with the location reagents ninhydrin, isatin, and iodoplatinate.

Results

There is a striking dichotomy in sulphur chemistry between *Calliandra* as circumscribed here, which includes members of Bentham's series *Macrophyllae, Nitidae,* and *Racemosae* (seed material of the small series *Pedicellatae* is not yet available for study), and the new genus *Za-*

Table 1. Distribution of sulphur-containing amino acids in seeds of species of *Zapoteca* compared with *Calliandra.* S-CEC = S-(β-carboxyethyl)-cysteine; S-CIC = S-(β-carboxyisopropyl)-cysteine; S-2 = uncharacterized amino acid.

Bentham Series	No. Species* Examined	Compounds S-CEC	S-CIC	S-2
Laetevirentes (*Zapoteca*)	8	−	−	++
Macrophyllae	8	+++	+	T
Nitidae	23	+++	+	T
Racemosae	8	+++	+	T

+++ = >10 mg/g dry wt; ++ = 1–10 mg/g dry wt; + = 0.1–1 mg/g dry wt; T = <0.1 mg/g dry wt; − = not detected.

* Species are listed by name, collection number, and herbarium where voucher is on file. Collectors: D = Delgado, DN = Neill, DS = Stevens, F = Forero, GR = Germplasm Resources Laboratory, Beltsville, MD, H = Hernández, J = Johnson, L = Lott, M = Martinez, MFR = Forero-Romeo, MS = Sousa, N = Nee, R = Robbertse, S = Shilom, SM = Smith, T = Torres.

Zapoteca

Z. caracasana J-2494, MO; *Z. formosa* T-4262, T-4063, MO; *Z. lambertiana* S-3405, MO; *Z. media* D-53, MO; *Z. portoricensis* H-154, H-465, MO; *Z. tetragona* J-2246-80, J-1532-80, H-800, H-827, MO; *Z.* sp. nov. (1), T-4167, MO; *Z.* sp. nov. (2) T-3947, MO.

Calliandra

Macrophyllae: C. angustifolia 15051, COL; *C. carbonaria* 33509, COL, SM-6471, MO; *C. glaberrima* 55261, 117125, F-9325, COL; *C. mexicana* 6064, USF; *C. rekoi* MS-12545, MO; *C. seemannii* 1860709, F; *C. tergemina* 156125, COL; *C.* aff. *tergemina* L-1684, L-1686, H-166, H-768, MO.

Nitidae: C. caeciliae 1765611, F; *C. depauperata* MFR-607, COL; *C. eriophylla* H-191, MO; *C. glomerulata* 15864, COL; *C. haematocephala* 3817, USF; *C. humilis* D-1201, MO; *C. magdalenae* N-23070, H-674, MO; *C. matisiana* 25785, COL; *C. medellinensis* F-9415, COL; *C. pittieri* 66977, COL; *C. pubiflora* MFR-603, COL; *C. purdiei* F-9955, COL; *C. purpurea* F-9920, 05360, COL; *C. redacta* R-1168, MO; *C. reticulata* 1437, TEX; *C. rigida* 52044, COL; *C. rubescens* DS-11139, H-762, H-763, J-12273 MO, 1633009 F; *C. schultzei* F-9419, F-9861, F-9888, F-9889, F-9890, F-9897 COL; *C. selloi* MFR-538 COL; *C. tenuiflora* 133081, COL; *C. tolimensis* 14913, COL; *C. turbinata* 128406, COL; *C.* sp. nov. (1), H-867, MO.

Racemosae: C. calothyrsus GR s.n., MO; *C. grandiflora* H-113, T-4316, H-833, MO; *C. houstoniana* DN-5482, H-164, MO; *C.* aff. *houstoniana* M-6369, H-777, H-846, H-847, MO; *C.* sp. nov. (2), H-454, MO; *C. juzepezukii* H-400, MO; *C. parviflora* 1841137, F; *C. rusbyi* H-865, MO.

TABLE 2. Distribution of imino acids in leaves and seeds of *Zapoteca* species. TT (trans-trans), CC (cis-cis), TC (trans-cis), CT (cis-trans)-dihydroxypipecolic acid; C4 (cis-4), T4 (trans-4), C5 (cis-5), T5 (trans-5)-hydroxypipecolic acid; PIP—pipecolic acid.

Species	Col. No.	TT	CC	TC	CT	C4	T4	C5	T5	PIP
Z. caracasana	J-2494	++					++	+		+
Z. formosa	T-4262	++					+	++		++
	T-4063	++					+	+		+
Z. lambertiana	S-3405	++					++	++		+++
Z. media	D-53	++					+	+		
Z. mollis	G-4164	++	++				+			+
Z. portoricensis	H-154	++				+		++		+
	H-465	++				+		++		+
Z. tetragona	J-2246-80	++					++	++		
	J-1532-80	++					++	++		
	H-800	++				+	++	++		+
	H-827	++				+	++	++		+
Z. sp. nov. 1	T-4167	++					+	+++		
Z. sp. nov. 2	T-3947	++					+	++		

+++ = >1 mg/g dry wt; ++ = 0.1–1 mg/g dry wt; + = <0.1 mg/g dry wt.

poteca, which includes those members of *Calliandra* belonging to Bentham's series *Laetevirentes.* All species of *Calliandra* that have been examined contain S-CEC as the major free seed amino acid (Table 1). This compound accounts for as much as 2.5% of the total seed weight. S-CEC has not been detected at all in members of *Zapoteca* (Table 1). The distribution of a second compound, S-CIC, which is found in much lower concentrations, follows the same pattern. Conversely, another nonprotein amino acid (S-2), as yet unidentified because of insufficient material but believed to be a sulphur compound, is the major free amino acid of *Zapoteca.* This compound is lacking or present only in trace amounts in *Calliandra* (Table 1).

The distributional data for the imino acids of *Zapoteca* are shown in Table 2. The presence of large amounts of trans-trans-4,5-dihydroxypipecolic acid together with the monohydroxypipecolic acids trans-4- and cis-5- is the common pattern. The dihydroxy isomer contains the same absolute configuration about the 4- and 5-carbons as the monohydroxy isomers with which it most frequently co-occurs. This *Zapoteca* pattern is one of several different combinations of mono and dihydroxy compounds that are seen in *Calliandra* species (Romeo, 1984 and unpubl. data). Of the other three dihydroxypipecolic acid isomers that may characterize some sections of *Calliandra,* only the cis-cis isomer was detected in significant concentrations in one species of *Zapoteca.*

DISCUSSION

Nonprotein amino acids are useful as chemical systematic markers in legumes (see Bell, 1971, and Harborne & Turner, 1984 for reviews). Some taxa have been characterized by the accumulation of a single unusual amino acid. For example *Mucuna* species are distinguished by the accumulation of large amounts of L-3,4-dihydroxyphenylalanine (Bell & Janzen, 1971), and 5-hydroxy-L-tryptophan is found only in species of *Griffonia* (Bell et al., 1976). More often, however, it is an association of nonprotein amino acids that characterizes a taxon. Biochemical subgeneric groupings have been established for *Lathyrus* and *Vicia* (Bell, 1971), and *Acacia* (Seneviratne & Fowden, 1968; Evans et al., 1977). Recently, a reassessment of four major genera (*Derris, Tephrosia, Lonchocarpus,* and *Millettia*) of the Tephrosieae (Fabaceae) was suggested by studies of the distribution of basic nonprotein amino acids in this group (Evans et al., 1985).

The significance of the findings reported herein is difficult to evaluate for several reasons: 1) a limited number of species have been examined for sulphur compounds (8 of 18 taxa of *Zapoteca,* 39 of the ca. 200 species of *Calliandra*). Bentham's four major series are well represented in this group, however, and many species are represented by more than one sample (Table 1); 2) some chemical identities and the metabolic pathways of the secondary compounds are not yet known; 3) relationships within the large genus *Calliandra* are still unclear, and a suitable mor-

phological framework upon which to base chemical interpretation does not exist. Nonetheless, tentative judgements can be made. The sulphur amino acid patterns are distinctive enough that, on the basis of these data alone, one can assign species to one or the other group with a reasonable amount of certainty. When considered together with the palynological data (Guinet, 1965, 1969; Nevling & Elias, 1970; Niezgoda et al., 1983) and the morphological, cytological, ecological, and developmental findings (Hernández, 1986), these chemical data can be viewed as support for the segregation of the *Zapoteca* species from *Calliandra*.

The imino acid pattern of *Zapoteca,* in contrast, while generally consistent within the genus, is not a particularly distinctive one vis à vis *Calliandra*. Imino acid patterns observed in *Calliandra* consist primarily of the absence or presence of one or more dihydroxypipecolic acid isomers in association with the monohydroxylated compounds that are the probable precursors of those isomers. All four possible dihydroxy compounds have discontinuous distributions within *Calliandra*. The usual trans-trans, trans-4, cis-5 pattern of *Zapoteca* is common in *Calliandra* and is found in several Latin American species. This sharing of rare imino compounds emphasizes the close phyletic relationship of *Zapoteca* to *Calliandra* just as the differing sulphur amino acids emphasize their distinctness. Since the distribution of these compounds is not known from other related genera (*Inga, Lysiloma, Pithecellobium*), it is not yet possible to speculate about the apomorphic or plesiomorphic nature of the chemical characters. As the metabolic relationships of the various compounds become elucidated, and as interspecific relationships within *Calliandra* itself become better understood with systematic revision, we can expect new phylogenetic insight into the relationship of *Zapoteca* to *Calliandra*.

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A COMPARATIVE STUDY OF THE EMBRYOLOGY OF *LUDWIGIA* (ONAGRACEAE): CHARACTERISTICS, VARIATION, AND RELATIONSHIPS[1]

HIROSHI TOBE[2] AND PETER H. RAVEN[3]

ABSTRACT

Based on our examination of samples representing seven sections, 11 species, and up to 40 characters, we describe the embryological characteristics of the genus *Ludwigia* (Onagraceae). *Ludwigia* represents a phylogenetic line separate from all other Onagraceae, so it occupies a key position in considerations of relationships within the family and between Onagraceae and other families of Myrtales. The typical distinctive 4-nucleate *Oenothera*-type embryo sac was present in all species studied, displaying no distinctive features. The embryo sacs of Myrtales, including Onagraceae and Lythraceae, lack antipodal cells at maturity. This character cannot therefore be used to demonstrate relationships between these families, as suggested by earlier embryologists. Two derived embryological features that are shared by Onagraceae and Lythraceae, however, and might indicate relationships between them are (1) the ubiquitous occurrence of starch grains in the nucellus; and (2) tracheidal exotegmens. Among the embryological features that we examined in *Ludwigia,* seed coat anatomy may be most useful in considering relationships within the genus. For example, the specialized endotestal structure of sect. *Dantia* is found only in members of sect. *Microcarpium,* thus supporting the hypothesis that the two sections are closely related.

Despite the fact that it clearly belongs in the order Myrtales, Onagraceae is very distinctive within that order (Cronquist, 1981; Dahlgren & Thorne, 1984; Johnson & Briggs, 1984). One of the most distinctive aspects of the family is its embryology, and in particular its unique 4-nucleate *Oenothera* type embryo sac (Seshavataram, 1970; Raven, 1979; Tobe & Raven, 1983). Within Onagraceae, the genus *Ludwigia,* consisting of about 80 species found mainly in the tropics and in temperate North America, is the only genus of tribe Jussiaeeae (Raven, 1979). *Ludwigia* has been studied intensively from various points of view, partly because it has been considered to be a primitive group, closest to a prototype of Onagraceae (see Parmentier, 1897; Melchior, 1964; Takhtajan, 1980). Earlier studies of *Ludwigia* have been concerned with biosystematics (Duke, 1955; Schmidt, 1967; Ramamoorthy & Zardini, 1987; Peng, 1982); chromosomal observations (Gregory & Klein, 1960; Kurabayashi et al., 1962; Raven & Tai, 1979); pollen morphology (Skvarla et al., 1975, 1976, 1978); reproductive morphology and anatomy (Eyde, 1977, 1978, 1981); and leaf anatomy (Keating, 1982). These works as a whole have indicated both the intersectional diversity of *Ludwigia* and its distinctiveness as a genus.

Eyde (1981) provided a comprehensive review of the interrelationships of the sections of *Ludwigia.* He suggested, based on his analysis of its characteristics, that *Ludwigia* is the sister group of all other Onagraceae, a concept that is well supported by evidence drawn from many different lines of investigation.

The present study is concerned with the embryological characters of the genus; i.e., the development of anthers, ovules, embryos, seeds, and gametophytes. All of these characters have been poorly investigated in the past. Eleven species representing seven sections, selected to represent the range of variation in the genus, have been examined in detail. This study is intended to illuminate the pattern of variation in embryological characteristics within the genera, and to provide a sound basis for comparisons with other members of the family Onagraceae and the order Myrtales.

REVIEW OF EARLIER EMBRYOLOGICAL STUDIES

Anthers and microspores. Seshavataram (1967, 1970) described these features in *Lud-*

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wigia octovalvis (Jacq.) Raven. The anther wall is six-layered and consists of the epidermis, fibrous endothecium, three middle layers, and the tapetum; the tapetum is glandular, and its cells are two-nucleate; cytokinesis in the microspore mother cells is simultaneous. No other details were described.

Ovule and megagametophyte formation. Täckholm (1915) reported the presence of the 4-nucleate *Oenothera* type embryo sac in *Ludwigia octovalvis* (Jacq.) Raven (= "*Jussieua* cfr. *villosa* Lam.," "*J.* cf. *suffruticosa* DC."). His report came only a few years after Geerts (1908) first detected this unique type in *Oenothera glazioviana* Mart. (= *O. lamarckiana* de Vries). Subsequent papers dealt with *L. peploides* (HBK.) Raven (= "*Jussieua repens*"; Ishikawa, 1918); *L. adscendens* (L.) Hara (= "*Jussieua repens*"; Maheshwari & Gupta, 1934; Khan, 1942); *L. epilobioides* Maxim. (= "*L. prostrata*"; Ishikawa, 1918); *L. perennis* L. (= "*L. parviflora*"; Maheshwari & Gupta, 1934); and again with *L. octovalvis* (Seshavataram, 1967, 1970). Taken together, these papers indicate that in *Ludwigia* the ovule in anatropous, bitegmic, and crassinucellate; the micropyle is formed by both integuments; the archesporium is one-celled (in most reports) or multi-celled (Khan, 1942); an archesporial cell cuts off the primary parietal cell; the tetrads of megaspores are linear; the micropylar megaspore in the tetrad is functional and develops into a 4-nucleate *Oenothera* type embryo sac; and the chalazal megaspore may also develop to a certain degree, resulting in an additional rudimentary embryo sac in an ovule.

Fertilization and endosperm. Porogamous fertilization and Nuclear endosperm formation were reported in *Ludwigia octovalvis* (= "*Jussieua* cfr. *villosa*"; Täckholm, 1915; Seshavataram, 1967, 1970) and *L. adscendens* (= "*Jussieua repens*"; Khan, 1942). Täckholm (1915) stated that the free endosperm nuclei became cellular only at the micropylar region, whereas Seshavataram (1970) observed that the endosperm became absolutely cellular. In this connection, Johansen (1931: 23) implied that *Ludwigia,* which he considered a primitive genus, had a dense and distinctly cellular endosperm as a heritage from its ancestor, whereas *Epilobium* (= "*Zauschneria*"), an advanced genus, had a coenocytic endosperm, or no endosperm at all at maturity.

Hypostase. Täckholm (1915) first simply described that a hypostase was differentiated in *Ludwigia octovalvis* (= "*Jussieua* cfr. *villosa*"). A later paper that was concerned with *L. peploides* (= "*Jussieua repens*") and *L. epilobioides* (= "*L. prostrata*"; Ishikawa, 1918) reported that a hypostase was absent. Later, Johansen (1928a, 1928b) declared that there was no hypostase in *Ludwigia,* based on the observations of a *Ludwigia* that he called *L. mullertii.* He contrasted its absence in *Ludwigia* with its presence in such genera as *Oenothera, Gaura,* and *Clarkia.* Johansen explained the function of the hypostase (and the epistase) as follows: "They serve to stabilize the water balance of the resting seed over the long period of dormancy during the hot dry season." Maheshwari and Gupta (1934) did not observe the hypostase in *L. perennis* L. (= "*L. parviflora*") and *L. adscendens* (L.) Hara (= "*Jussieua repens*") either. In contrast, Khan (1942) reported that in *L. adscendens* (= "*Jussieua repens*") neither a hypostase nor an epistase is present in the young ovules, but that a conspicuous hypostase was formed subsequently. Seshavataram (1967) confirmed the presence of a hypostase in the older stages of development of the ovule of *L. octovalvis.*

Starch grains in the nucellus. Ishikawa (1918) first described starch grains in the nucellus of Onagraceae. He reported that the starch grains were rather infrequent in *L. epilobioides* (= "*L. prostrata*") and few in *L. adscendens,* in contrast with their abundance in *Oenothera, Gaura,* and *Circaea.* Because of his belief that *Ludwigia* lacked a hypostase, Ishikawa inferred that its presence was correlated with a lack of starch grains in the nucellus.

Embryogeny. Only the Onagrad type of embryogeny has been recorded in *Ludwigia.* Reports include those of Souèges (1935) for *L. palustris* (L.) Elliott, Khan (1942) for *L. adscendens*; and Seshavataram (1967, 1970) for *L. octovalvis.*

Seed coat. Corner (1976) first gave general descriptions of the seed coat histology of *Ludwigia* (= "*Jussieua*"), based on his observation of *L. peruviana* (L.) Hara (= "*Jussieua peruviana*"). The testa is two-layered with the endotesta composed of crystal cells that are lignified and stellately lobed with thickened inner and radial walls. The tegmen is also two-layered with the fibrous exotegmen. Eyde (1978) provided general descriptions of the seed coat histology of species of seven sections of *Ludwigia,* including *L. peruviana.*

This review of the available literature indicates clearly that, although quite a few reports on the embryology of *Ludwigia* have been published,

TABLE 1. Vouchers of the *Ludwigia* species used.

Species	Vouchers
Sect. *Myrtocarpus*	
L. peruviana (L.) Hara	Australia. Mascot District, Sydney, *B. G. Briggs 7143, 7226* (NSW).
Sect. *Macrocarpon*	
L. lagunae (Morong) Hara	Paraguay. Asunción, Luque, *T. P. Ramamoorthy 1019* (MO). Paraguay. Caaguazú, *T. P. Ramamoorthy 1097* (MO).
L. bonariensis (Michx.) Hara	Argentina. Buenos Aires, *T. P. Ramamoorthy 1005* (MO). Argentina. Tucumán, *T. P. Ramamoorthy 1015* (MO).
Sect. *Ludwigia*	
L. maritima Harper	USA. South Carolina, Colleton Co., *C. Peng 3920* (MO).
L. virgata Michx.	USA. Alabama, Mobile Co., *H. Tobe s.n.* (MO).
Sect. *Microcarpium*	
L. lanceolata Elliott	USA. Georgia, McIntosh Co., *C. Peng 4139* (MO).
L. glandulosa Walter subsp. *glandulosa*	USA. Louisiana, Cameron Parish, *C. Peng 4367* (MO).
Sect. *Dantia*	
L. repens Forster	USA. Florida, Lee Co., *C. Peng 4290* (MO).
L. arcuata Walter	USA. Florida, Hillsborough Co., *C. Peng 4320* (MO).
Sect. *Seminuda*	
L. leptocarpa (Nutt.) Hara	Brazil. Bentos, Santa Catarina, *T. P. Ramamoorthy 1134* (MO). USA. Georgia, Barnwell Co., *R. W. Dolan 1* (MO).
Sect. *Oligospermum*	
L. peploides (Kunth) Raven	USA. Missouri, St. Louis Co., *H. Tobe s.n.* (MO).

there still remain several gaps in the available information. Also, the discrepancies in literature regarding the ovular archesporium, the endosperm, and the hypostase remain to be resolved.

MATERIALS AND METHODS

The 11 species examined in this study are listed in Table 1, together with voucher informa-

TABLE 2. A summary of embryological data on anthers and microspores.

Taxa	Thickness of Anther Wall	Type of Anther Wall Development	Tapetum	Nuclear Number of Tapetal Cell	Delimitation of Microspores	Endothecium	Epidermis	Microspore Tetrads[1]	Cell Number in Mature Pollen
Sect. *Myrtocarpus*									
L. peruviana	5–6 layers	Basic	glandular	2-nucleate	simultaneous	fibrous	persistent	usually tetrahedral/ rarely decussate/ very rarely isobilateral	2-celled

TABLE 2. Continued.

Taxa	Thickness of Anther Wall	Type of Anther Wall Development	Epidermis	Endothecium	Tapetum	Nuclear Number of Tapetal Cell	Delimitation of Microspores	Microspore Tetrads[1]	Cell Number in Mature Pollen
Sect. *Macrocarpon*									
L. lagunae	5 layers	Basic	persistent	fibrous	glandular	2-nucleate	—	usually tetrahedral/very occasional decussate/rarely isobilateral	2-celled
L. bonariensis	5–6 layers	Basic	persistent	fibrous	glandular	2-nucleate	simultaneous	—	2-celled
Sect. *Ludwigia*									
L. maritima	—	—	—	—	—	—	—	—	2-celled
L. virgata	5–6 layers	Basic	persistent	fibrous	glandular	2-nucleate	simultaneous	—	2-celled
Sect. *Microcarpium*									
L. lanceolata	5 layers	Basic	persistent	fibrous	glandular	2-nucleate	simultaneous	usually tetrahedral/occasionally decussate	2-celled
L. glandulosa subsp. *glandulosa*	5 layers	Basic	persistent	fibrous	glandular	2-nucleate	simultaneous	usually tetrahedral/very occasionally decussate	2-celled
Sect. *Dantia*									
L. repens	5 layers	Basic	persistent	fibrous	glandular	2-nucleate	simultaneous	usually tetrahedral/occasionally decussate	2-celled
L. arcuata	5–6 layers	Basic	persistent	fibrous	glandular	2-nucleate	simultaneous	—	2-celled
Sect. *Seminuda*									
L. leptocarpa	5 layers	Basic	persistent	fibrous	glandular	2-nucleate	simultaneous	nearly always tetrahedral/rarely decussate	2-celled
Sect. *Oligospermum*									
L. peploides	5–6 layers	Basic	persistent	fibrous	glandular	2-nucleate	—	—	2-celled

[1] Based on 50 selected tetrads. Expressions for frequency follow Schmid (1982).

tion. The samples of flower buds and fruits in various stages of development were fixed with FAA (5 parts stock formalin; 5 parts glacial acetic acid; 90 parts 70% ethanol). Subsequently, they were dehydrated through a *t*-butyl alcohol series, and then embedded in Paraplast with melting point 57–58°C for microtome sectioning. Serial sections cut 5–7 μm in thickness were stained with Heidenhain's hematoxylin, safranin, and fast green FCF, and mounted in Histoclad.

Observations of microtome sections were made with a Zeiss Standard microscope equipped with a phase-contrast condenser. The photomicrographs were mostly taken using an Iris diaphragm for bright-field observations. In some, annular stops were used for the phase-contrast observations in order to show the location of starch grains in the nucellus (e.g., Figs. 8–12, 15, 16).

RESULTS

Embryological data concerning all species studied are summarized and compared in Tables 2–6. A discussion of these characteristics is presented in the following pages.

ANTHERS AND MICROSPORES (TABLE 2)

The thickness of anther wall varies from five to six cell layers (Fig. 1). There is no conspicuous difference in thickness from species to species, nor from section to section. The anther wall is composed of an epidermis, an endothecium, two or three middle layers, and a tapetum (Fig. 1). Following the definitions of types by Davis (1966: 8–11), the wall formation of all the species studied conforms to the Basic type. In it, the middle layers have a common histogenetic origin with both the endothecium and the tapetum (Fig. 1).

As the anther develops, the middle layers are completely crushed (Fig. 2). The epidermis is persistent and remains uncrushed until the time of anther dehiscence; in some species such as *Ludwigia leptocarpa* (Fig. 3) and *L. peploides*, the epidermal cells are more or less flattened, but in most other species, they are enlarged as much as the endothecial cells (Fig. 4). The endothecium always develops fibrous thickenings, as shown by Eyde (1977). The tapetum is glandular and its cells become two-nucleate.

Meiosis in the microspore mother cells is accompanied by simultaneous cytokinesis (see arrow in Fig. 2), as recorded in *L. octovalvis* (Seshavataram, 1967, 1970). The arrangement of microspores in a tetrad is usually tetrahedral, occasionally decussate, and rarely isobilateral throughout the genus; there is no conspicuous difference in the frequencies of the different types of arrangement from species to species. The pollen grains are two-celled when shed (Fig. 5).

OVULES (TABLE 3)

The characteristics of the ovule are remarkably consistent throughout the genus: the ovule is anatropous, crassinucellate, and bitegmic. The inner integument is always two-layered. The outer integument is two-layered in most species but is three-layered in its basal portion in *Ludwigia peploides* (sect. *Oligospermum*). The distinctive mode of initiation of the integuments in *L. peploides* is discussed in a separate paper (Tobe & Raven, 1985). The micropyle is always formed by both integuments.

MEGAGAMETOPHYTE FORMATION AND NUCELLUS (TABLE 4)

The archesporium is uniformly one-celled (Fig. 6), contrary to a report by Khan (1942), who wrote that it looked multicellular in *Ludwigia adscendens*. Very rarely, more than one megaspore mother cell (archesporial cell) is found in

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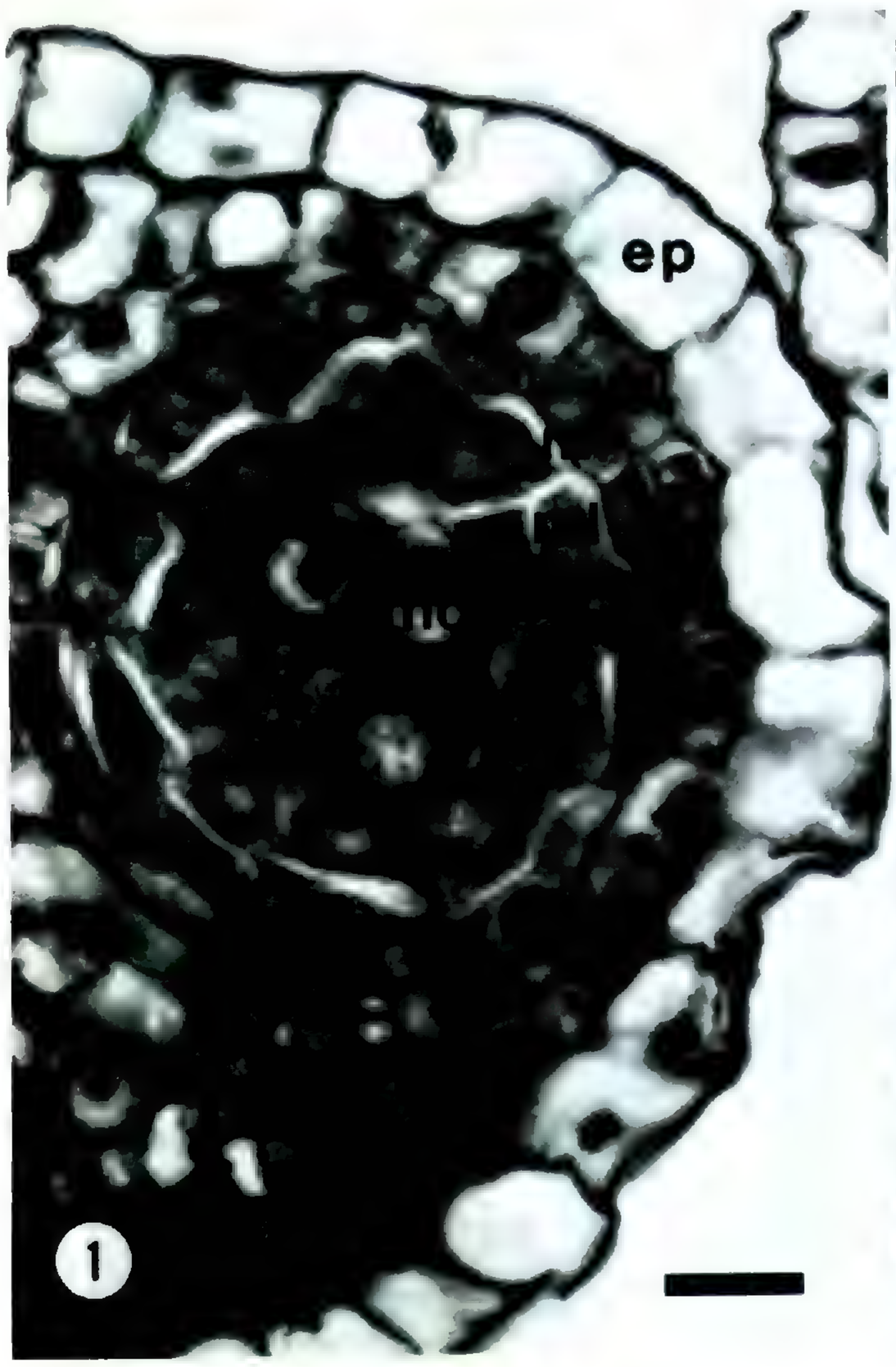
FIGURES 1–5. Anthers and microspores of *Ludwigia*.—1. *L. leptocarpa*. Transverse section (TS) of a young anther. The wall is 5-layered, consisting of epidermis (ep), endothecium (et), two middle layers (ml), and tapetum (t) (mc = microspore mother cell). Scale = 10 μm.—2. *L. bonariensis*. TS of an older anther showing collapsed middle layers and 2-nucleate glandular tapetal cells (t); epidermis (ep), endothecium (et). An arrow indicates cell at telophase of meiosis II. Scale = 50 μm.—3. *L. leptocarpa*. TS of a dehisced anther. The wall is composed of a flattened persistent epidermis (ep) and a fibrous endothecium (et). Scale = 100 μm.—4. *L. linearis* (*Dille 420*, MO). TS of a dehisced anther. The wall is composed of well-developed persistent epidermis (ep) and a fibrous endothecium (et). Scale = 100 μm.—5. *L. leptocarpa*. Two-celled pollen grain artificially separated from the normal tetrad formation found at dehiscence; stained with 1% aceto-carmine. Arrows indicate a large vegetative nucleus and a smaller generative one. Scale = 50 μm.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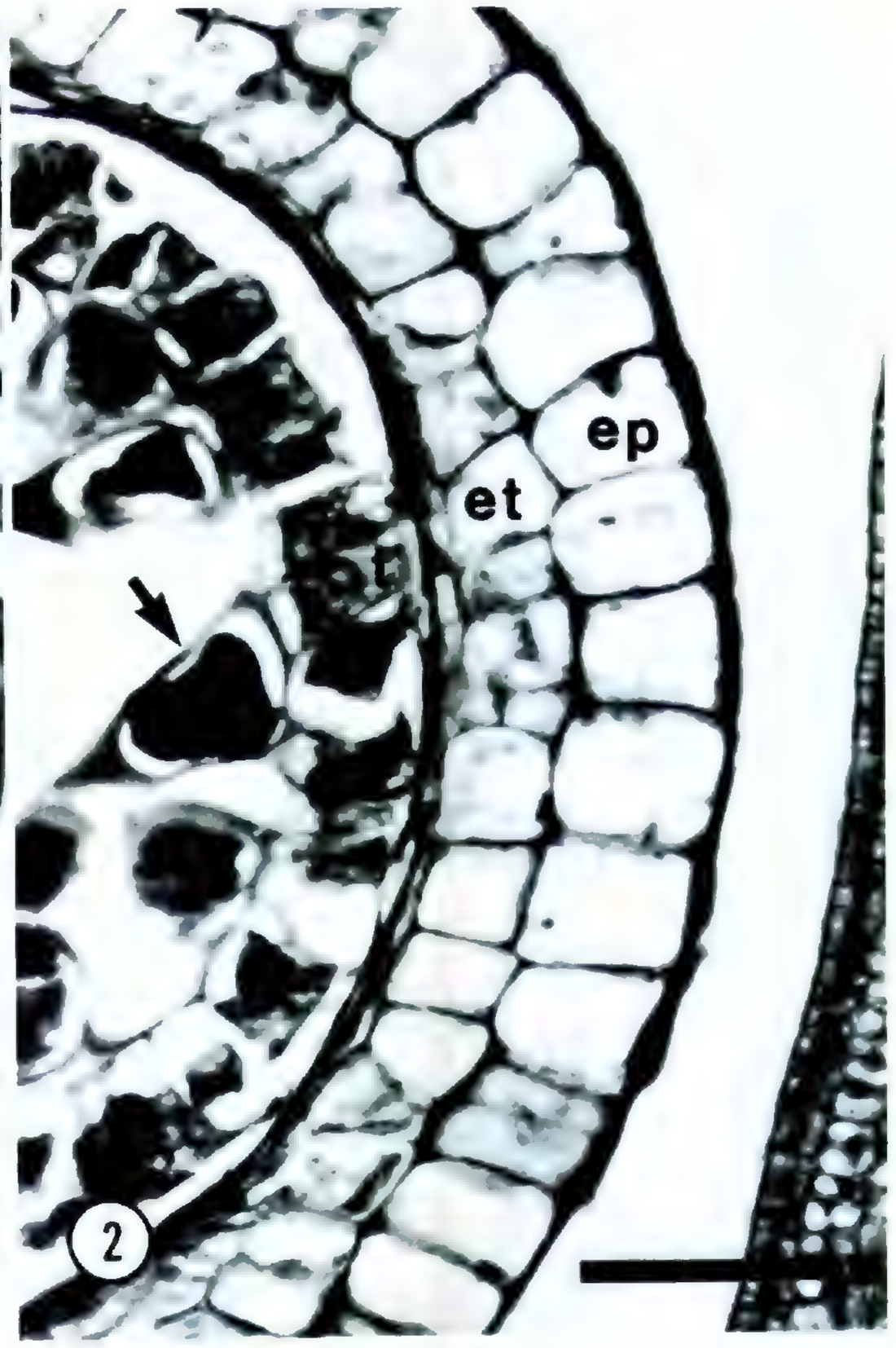
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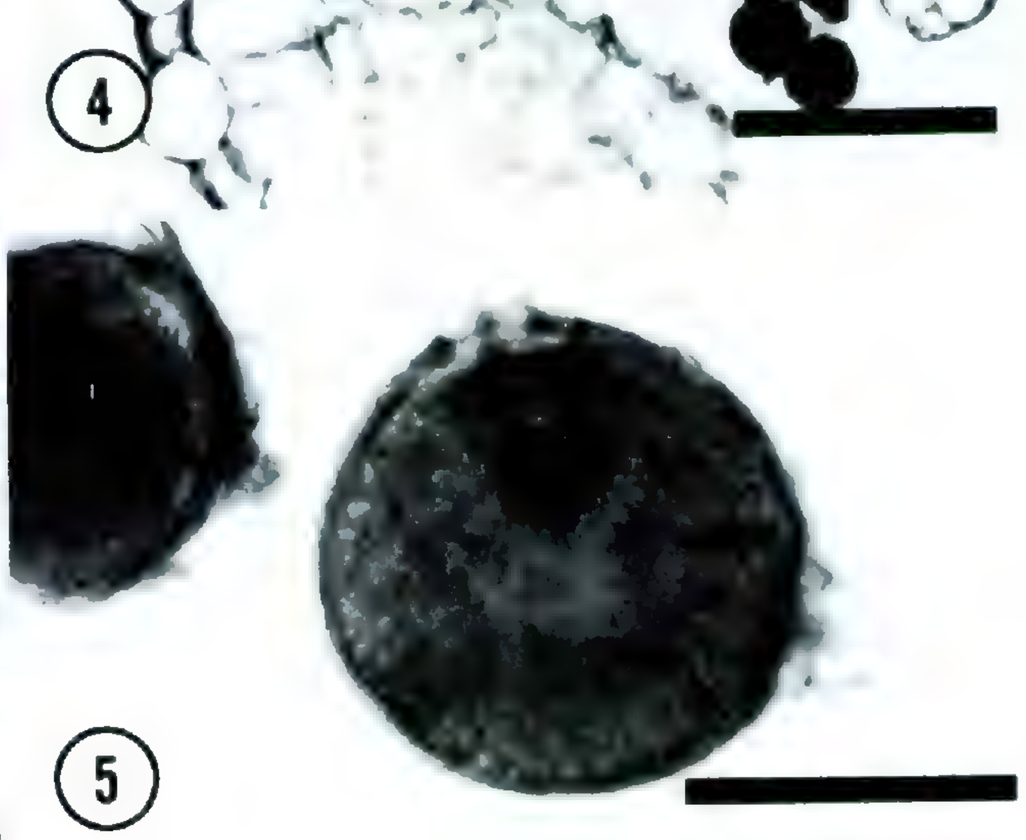
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TABLE 3. A summary of embryological data on ovules. Abbreviations: ii, inner integument; oi, outer integument.

Taxa	Ovule Type	Nature of Nucellus	Number of Integu-ments	Thickness of ii	Thickness of oi	Formation of Micropyle	Starch Grains in the Nucellus
Sect. *Myrtocarpus*							
L. peruviana	anatropous	crassinucellate	2	2-layered	2-layered	ii and oi	present
Sect. *Macrocarpon*							
L. lagunae	anatropous	crassinucellate	2	2-layered	2-layered	ii and oi	present
L. bonariensis	anatropous	crassinucellate	2	2-layered	2-layered	ii and oi	present
Sect. *Ludwigia*							
L. maritima	–	–	2	–	–	–	–
L. virgata	anatropous	crassinucellate	2	2-layered	2-layered	ii and oi	present
Sect. *Microcarpium*							
L. lanceolata	anatropous	crassinucellate	2	2-layered	2-layered	ii and oi	present
L. glandulosa subsp. *glandulosa*	anatropous	crassinucellate	2	2-layered	2-layered	ii and oi	present
Sect. *Dantia*							
L. repens	anatropous	crassinucellate	2	2-layered	2-layered	ii and oi	present
L. arcuata	anatropous	crassinucellate	2	2-layered	2-layered	ii and oi	present
Sect. *Seminuda*							
L. leptocarpa	anatropous	crassinucellate	2	2-layered	2-layered	ii and oi	present
Sect. *Oligospermum*							
L. peploides	anatropous	crassinucellate	2	2-layered	2(–3)-layered	ii and oi	present

TABLE 4. A summary of embryological data on megagametophyte formation.

Taxa	Number of Archesporial Cells	Thickness of Parietal Tissue	Arrangement of Megaspore Tetrad	Position of Functional Megaspore	Type of Embryo Sac Formation	Number of Nuclei in Mature Embryo Sac	Shape of Mature Embryo Sac
Sect. *Myrtocarpus*							
L. peruviana	1	4–5 layered	linear	micropylar	*Oenothera*	4	ellipsoidal
Sect. *Macrocarpon*							
L. lagunae	1	4–6 layered	linear	micropylar	*Oenothera*	4	ovoid
L. bonariensis	1	4–5 layered	linear	micropylar	*Oenothera*	4	ovoid
Sect. *Ludwigia*							
L. maritima	—	—	—	—	—	—	—
L. virgata	1	4–5 layered	linear	micropylar	*Oenothera*	4	ovoid
Sect. *Microcarpium*							
L. lanceolata	1	4–5 layered	linear	micropylar	*Oenothera*	4	ellipsoidal
L. glandulosa subsp. *glandulosa*	1	4–6 layered	linear	micropylar	*Oenothera*	4	ellipsoidal
Sect. *Dantia*							
L. repens	1	4–5 layered	linear	micropylar	*Oenothera*	4	ellipsoidal
L. arcuata	1	4–5 layered	linear	micropylar	*Oenothera*	4	ellipsoidal
Sect. *Seminuda*							
L. leptocarpa	1	3–4 layered	linear	micropylar	*Oenothera*	4	spherical
Sect. *Oligospermum*							
L. peploides	1	5–6 layered	linear	micropylar	*Oenothera*	4	ellipsoidal

a given nucellus. This condition was not characteristic of any species examined. Each archesporial cell divides periclinally into two: the upper primary parietal cell and the lower primary sporogenous cell. The primary parietal cell further divides periclinally (Fig. 7). Its daughter cells repeatedly divide periclinally and anticlinally, which results in a three- to six-layered parietal tissue being formed above the young embryo sac. The primary sporogenous cell directly develops into a megaspore mother cell (Figs. 7, 8) that later undergoes meiosis, forming megaspores (Figs. 9–11).

Heterotypic division in the meiosis of the megaspore mother cell results in the production of a dyad usually composed of a larger micropylar and a smaller chalazal cell (Figs. 9, 10). This contrasts sharply with the situation in most angiosperms, in which a dyad consisting of a smaller micropylar cell and a larger chalazal cell is common. The subsequent homotypic division usually occurs in both micropylar and chalazal cells, resulting in the formation of a linear tetrad of megaspores. Occasionally, it occurs only in the micropylar cell, in which case a linear triad of megaspores is formed. In either a tetrad or a triad, the micropylar megaspore is always the largest cell, and the functional one (Fig. 11). This megaspore enlarges, while the others degenerate (Fig. 12). Occasionally, we have observed an enlarging chalazal megaspore opposite the enlarged micropylar megaspore, a condition that was reported repeatedly in earlier works (e.g., Ishikawa, 1918). We have never observed twin mature embryo sacs derived from both the micropylar and the chalazal megaspore, however, nor have we ever seen a single mature embryo sac derived from the chalazal megaspore alone.

The functional megaspore undergoes two successive nuclear divisions, forming a megagametophyte. As has often been indicated in the earlier works, the nucleus of the functional megaspore moves toward the micropylar side before the first nuclear division; the two nuclei resulting from its first meiotic division remain on the micropylar side (see Fig. 13), with one slightly above the other. In the second nuclear division, the upper nucleus divides horizontally, whereas the lower one divides vertically (Fig. 13). It appears that the two nuclei derived from the upper nucleus develop into the two synergids, whereas those derived from the lower nucleus develop into the egg and the polar nucleus, as mentioned by Khan (1942). Thus, megagametophyte formation in *Ludwigia* conforms exactly to the *Oenothera*-type: the organized embryo sac contains the egg, two synergids and one polar nucleus, and lacks any antipodal cells (Figs. 15, 16). Very rarely an embryo sac with more than four nuclei is formed when other megaspores, which normally would have degenerated, are released from the nucellus into the embryo sac (Fig. 14). Such an aberrant embryo sac clearly does not indicate any similarity to any other type.

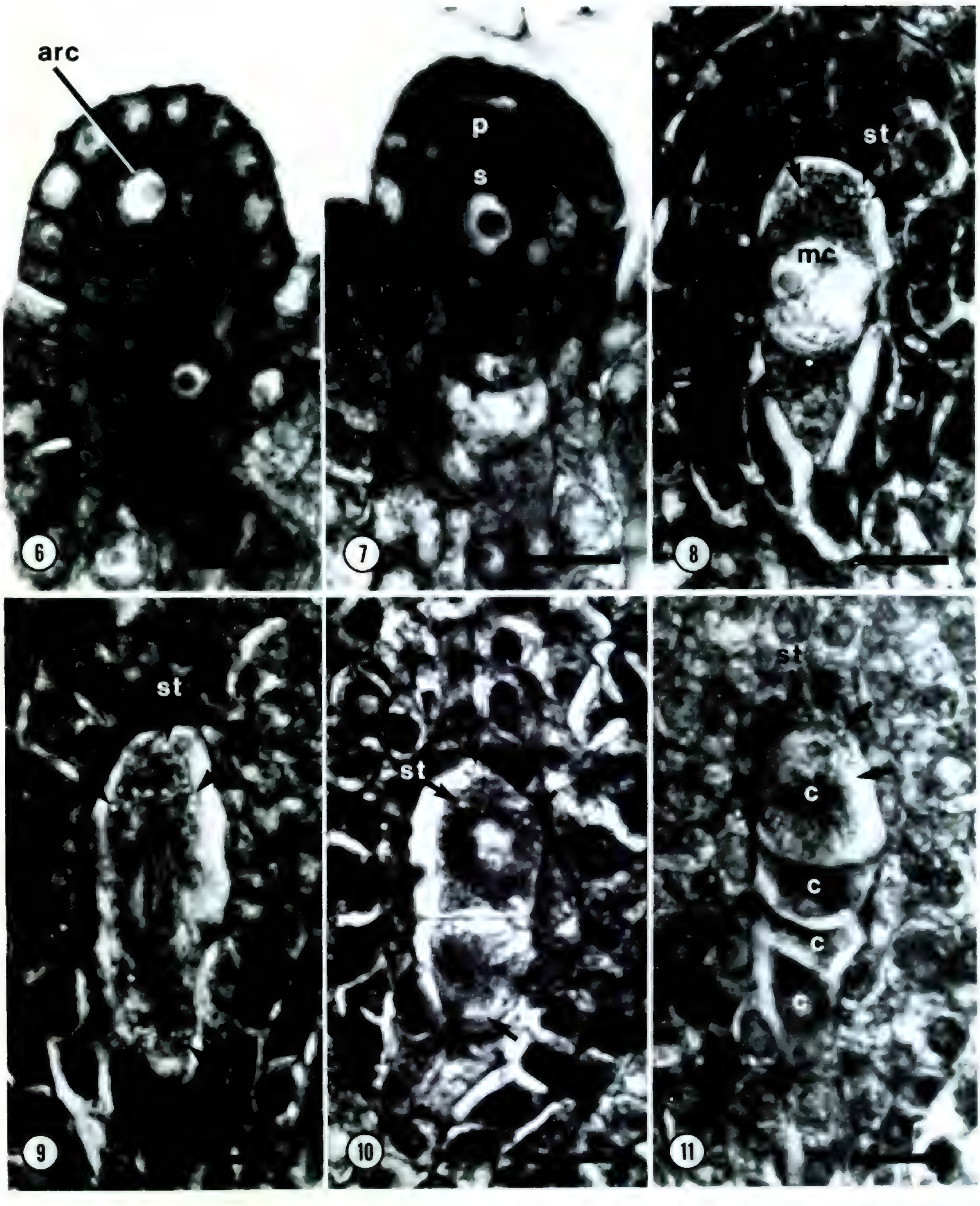
In *Ludwigia,* the mature embryo sacs are diverse in shape, varying from spherical or ovoid to ellipsoidal. There seem to be no significant differences in the shape of the mature embryo sac from one species to another, however.

During megasporogenesis and megagametogenesis, no particular specialization occurs in the nucellar tissue. Apical epidermal cells of a nucellus do not divide periclinally. This character is significant because the more or less related members of the Myrtales (e.g., Combretaceae) show remarkable periclinal divisions of the nucellar apical epidermal cells to form a nucellar cap (see Venkateswarlu & Rao, 1972).

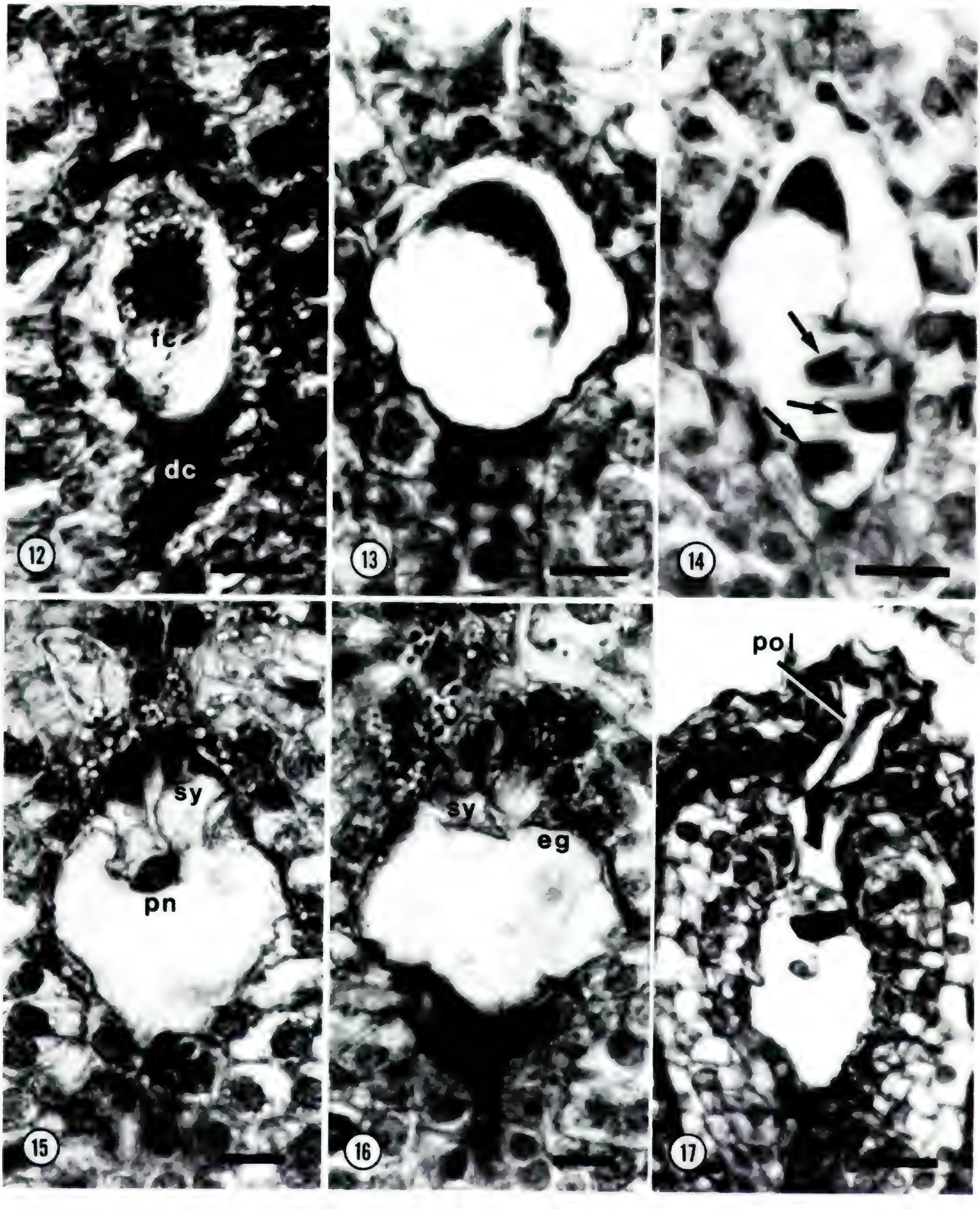
STARCH GRAINS (TABLE 3)

The accumulation of starch grains in the nucellar tissues of all species of *Ludwigia* is conspicuous, contrary to the observation of Ishikawa (1918). In some species—e.g., *L. virgata*—it is less conspicuous than in others. In the details of this process of starch accumulation, *Ludwigia* is exactly similar to *Epilobium* (Rodkiewicz & Bednara, 1974). Starch grains first appear on the upper, or micropylar side, of the megaspore mother cell (Fig. 8). During meiosis I, they are observed both on the micropylar and on the chalazal side, more abundantly on the former (Fig. 9). In the dyad stage, the starch grains of the upper cell are localized on the micropylar side, whereas those of the lower cell are restricted to the chalazal side (Fig. 10). In the tetrad, the functional megaspore, which is micropylar, has starch most abundantly on the micropylar side, while they disappear for the most part from the chalazal megaspore (Fig. 11). The two intervening megaspores have no starch grains.

At the functional megaspore stage numerous starch grains are observed not only within the functional megaspore but also in the nucellar tissue surrounding it (Fig. 12). As the ovule grows, more and more starch grains are accumulated in



FIGURES 6–11. Archesporium and megasporogenesis in *Ludwigia arcuata*. Longitudinal sections of young ovules from the archesporial cell stage to the megaspore tetrad stage. Arrows in 8–11 point out the location of plastids synthesizing starch grains (st). Scales = 10 μm.–6. Archesporial cell stage. Note that the archesporium (arc) is one-celled.—7. Primary sporogenous cell stage; primary parietal cell (p), primary sporogenous cell (s).—8. Megaspore mother cell stage; megaspore mother cell (mc).—9. Telophase of meiosis I.—10. Megaspore dyad stage.—11. Megaspore tetrad stage. Note that the micropylar megaspore (c) is larger than the lower three (c), and that starch grains are localized only in the micropylar megaspore.



FIGURES 12–17. Megagametogenesis and fertilization in *Ludwigia*. Longitudinal sections of older and fertilized ovules.—12. *L. arcuata*. Functional megaspore stage; functional megaspore (fc); remnant of degenerate megaspores (dc). Starch grains are scattered in the functional megaspore and in the nucellar tissue around it. Scale = 10 μm.—13. *L. peruviana*. Two-nucleate embryo sac stage. Note that the upper of the two nuclei is dividing horizontally and the lower vertically. Scale = 10 μm.—14. *L. virgata*. Unusual embryo sac composed of five nuclei, the lower (cellular) nuclei (arrow) being megaspores that should have degenerated. Scale = 10 μm.—15 and 16. *L. peruviana*. Two successive sections of a mature embryo sac consisting of an egg (eg), two synergids (sy), and one polar nucleus (pn). Note that numerous starch grains are scattered in the nucellar tissue. Scales = 10 μm.—17. *L. repens*. Fertilized ovule stage showing a remnant of a pollen tube (pol) penetrating into the micropyle. Scale = 20 μm.

TABLE 5. A summary of embryological data on fertilization, endosperm, embryo, and seed.

Taxa	Path of Pollen Tube	Type of Endosperm Formation	Cellular Endosperm	Endosperm in Mature Seed	Type of Embryogeny	Hypostase
Sect. *Myrtocarpus*						
L. peruviana	porogamous	Nuclear	formed	absent	—	present
Sect. *Macrocarpon*						
L. lagunae	porogamous	Nuclear	formed	absent	—	present
L. bonariensis	porogamous	Nuclear	formed	absent	Onagrad	present
Sect. *Ludwigia*						
L. maritima	porogamous	Nuclear	formed	absent	Onagrad	present
L. virgata	porogamous	Nuclear	—	—	—	—
Sect. *Microcarpium*						
L. lanceolata	porogamous	Nuclear	formed	absent	—	present
L. glandulosa subsp. *glandulosa*	porogamous	Nuclear	formed	absent	Onagrad	present
Sect. *Dantia*						
L. repens	porogamous	Nuclear	formed	absent	—	present
L. arcuata	porogamous	Nuclear	formed	absent	—	present
Sect. *Seminuda*						
L. leptocarpa	porogamous	Nuclear	formed	absent	—	present
Sect. *Oligospermum*						
L. peploides	porogamous	Nuclear	formed	absent	Solanad	present

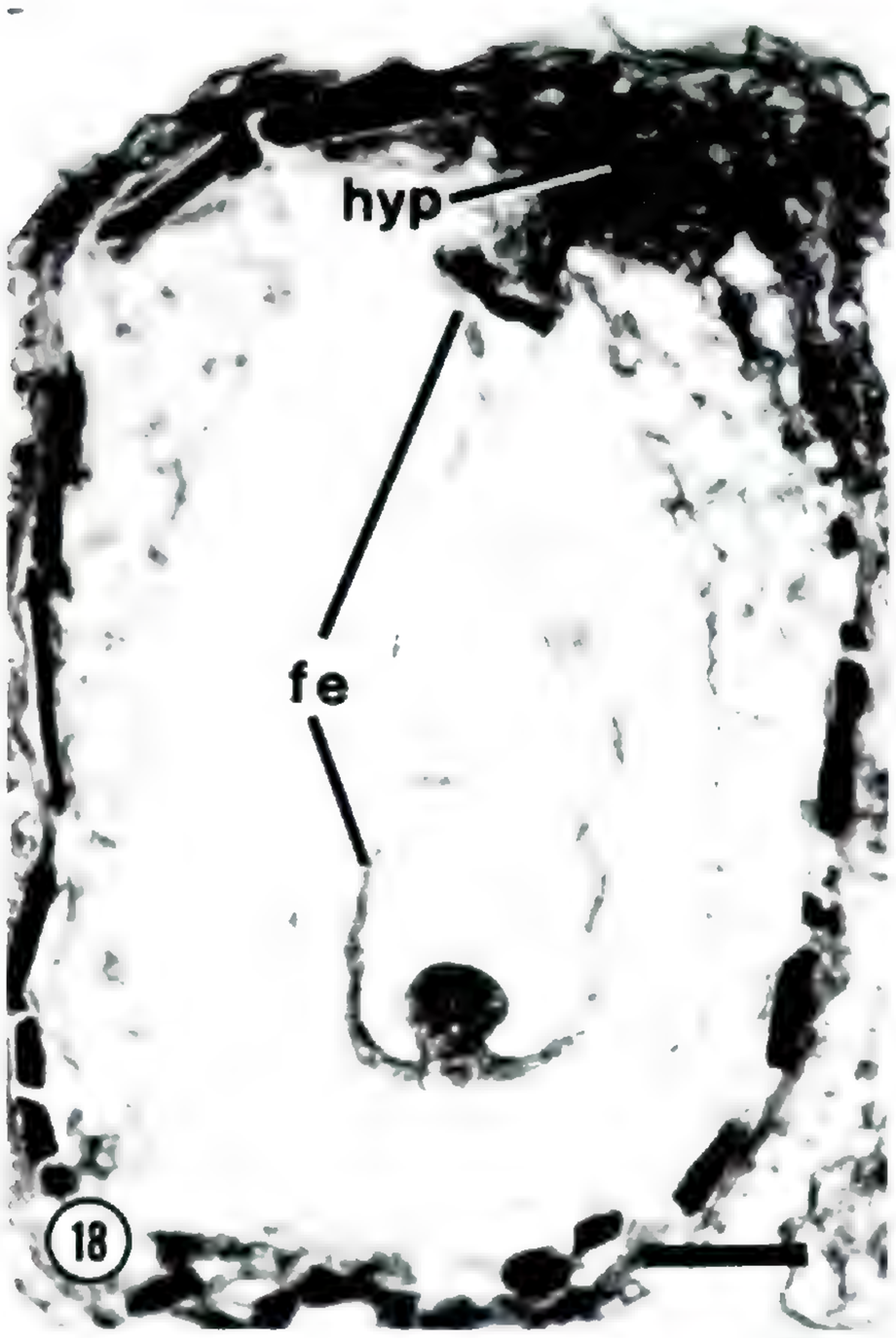
both the embryo sac and the nucellar tissue (Figs. 15, 16). Ultimately, starch grains are found abundantly even within the cells of the proembryo.

FERTILIZATION, ENDOSPERM, AND EMBRYO (TABLE 5)

Fertilization in *Ludwigia* is porogamous. We often observed a remnant of a pollen tube penetrating into the micropyle (Fig. 17).

Endosperm formation is of the Nuclear type (Fig. 18). During the early, free-nuclear stage, the endosperm nuclei form separate groups on the micropylar and the chalazal sides of the embryo sac, rather than being scattered peripherally (Fig. 18). At this stage, the endosperm nuclei on the chalazal side characteristically have dense cytoplasm and form a very obvious group (Fig. 18). Wall formation in the free endosperm nuclei always begins in the micropylar group, ultimately reaching the chalazal one. Cellular endosperm probably never fills the embryo sac, because the endosperm is apparently absorbed by the growing embryo more quickly than it is formed. Mature seeds in all Onagraceae completely lack endosperm (Fig. 23).

In a few species, we observed the details of embryogeny. *Ludwigia bonariensis, L. maritima,* and *L. glandulosa* all had the same Onagrad type embryogeny as reported in different species by all earlier workers (Souèges, 1935; Khan, 1942; Seshavataram, 1967, 1970). In *L. peploides* (sect. *Oligospermum*), however, the embryogeny was of the Solanad type. In both Onagrad and Solanad types, the basal cell of the two-celled proembryo plays only a minor or no part in the subsequent development of the embryo (Figs. 21, 22). The Solanad type differs from the Onagrad type in that the apical cell of the two-celled proembryo divides by a transverse wall (Fig. 20), instead of by a longitudinal wall as in the Onagrad type (Fig. 19). The suspensor is very short, mostly three or four cells long (Figs. 21, 22). The embryo in the mature seed is straight and has two equally developed cotyledons (Fig. 23).



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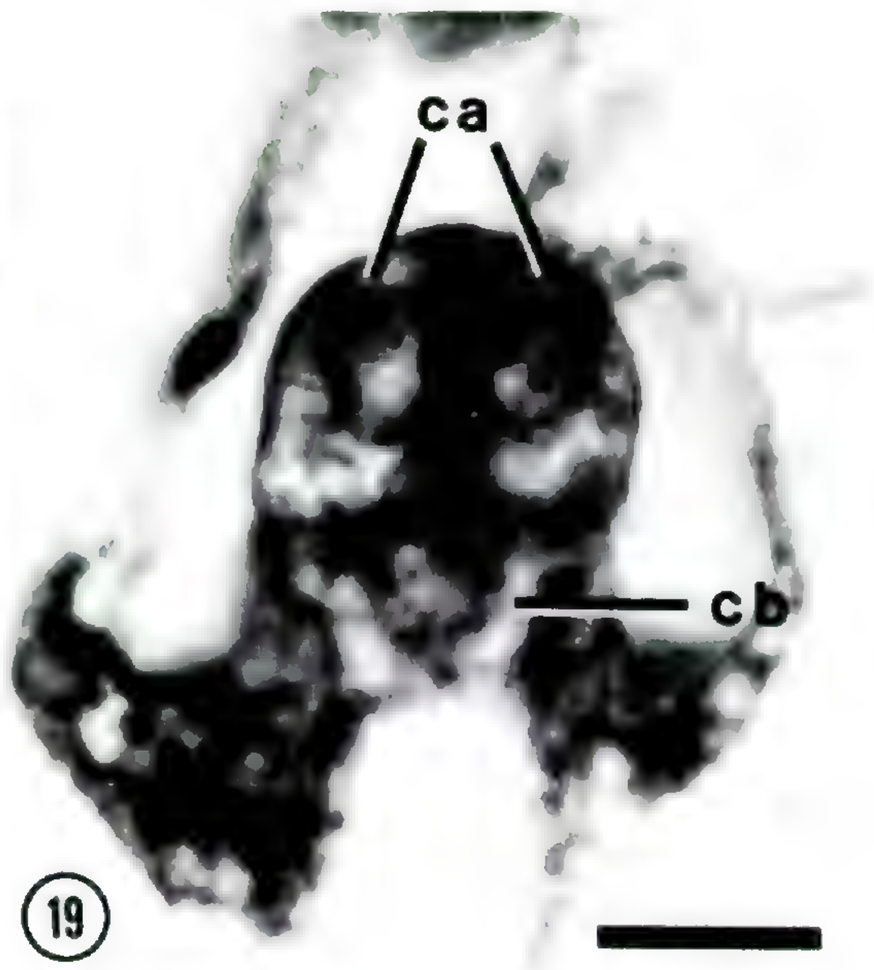

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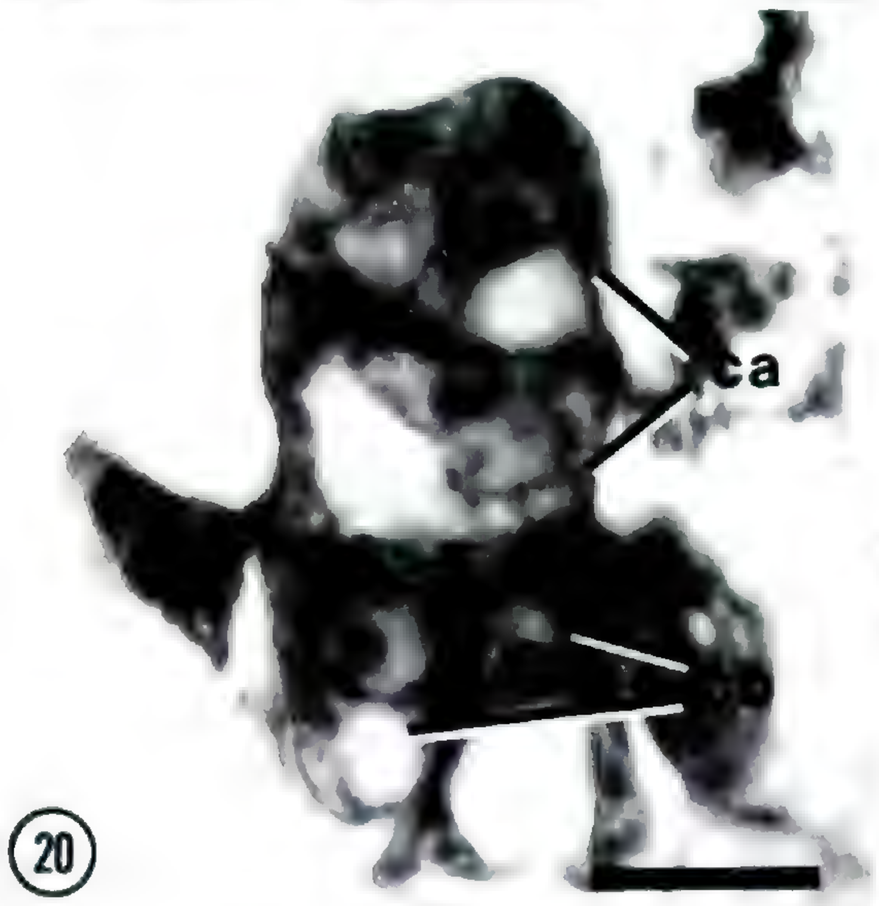

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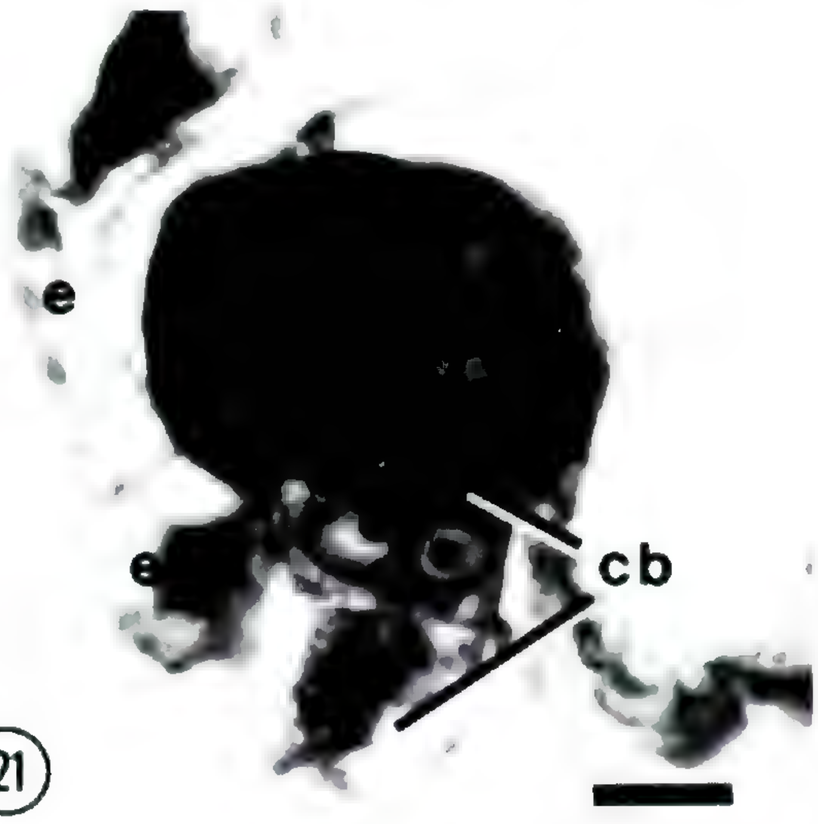

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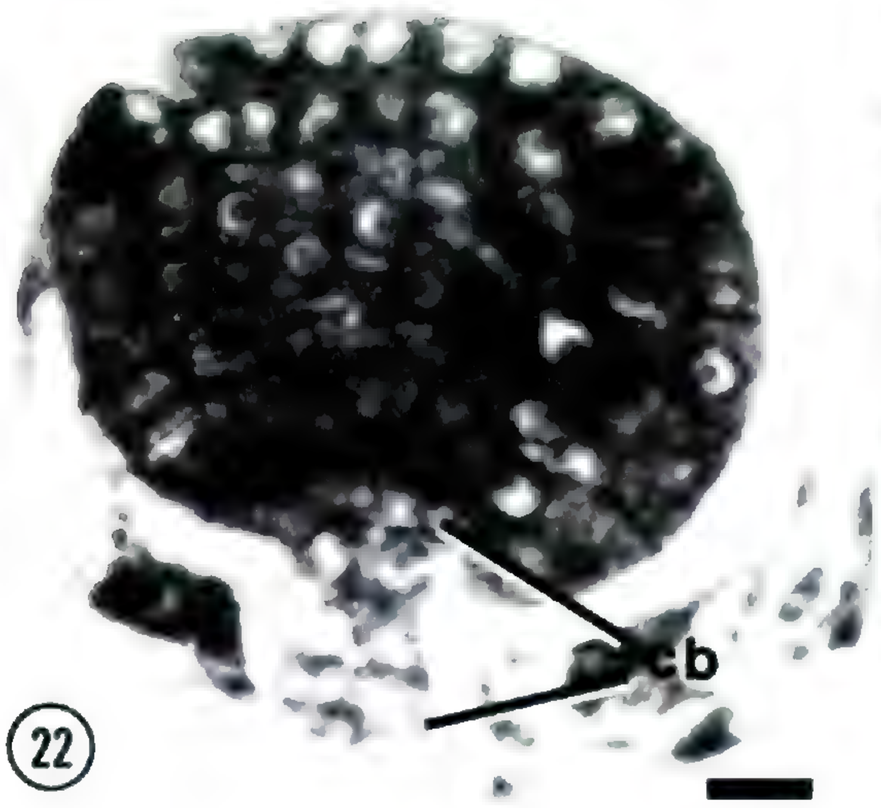

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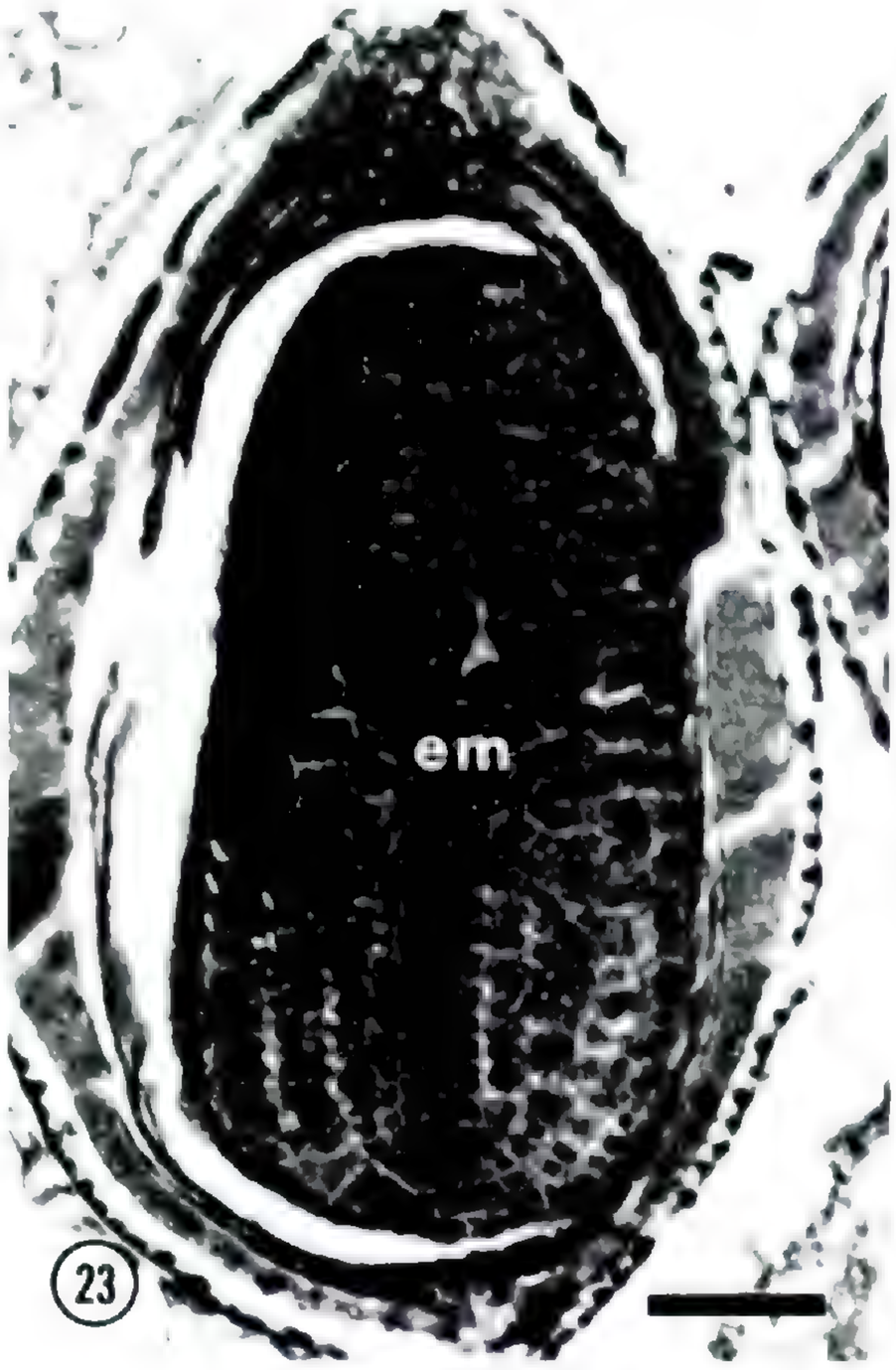

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FIGURES 18–23. Endosperm formation and embryogeny in *Ludwigia*. — 18. *L. maritima*. Longitudinal section (LS) of a young seed showing free endosperm nuclei (fe) and hypostase (hyp). Scale = 50 μm. — 19. *L. maritima*.

HYPOSTASE (TABLE 5)

In all of the species that we studied, we were able to confirm that the differentiation of the hypostase "consists of a well defined but irregularly outlined group of thick-walled cells at the chalazal end of the ovule" (Johansen, 1928a; see also Fig. 18). The hypostase was not observed, however, until the two- to four-celled proembryonal stage, at the earliest. In this respect, our results agree with those of Khan (1942) and Seshavataram (1968), who mentioned that the hypostase is not differentiated in younger ovules.

Starch grains appear in early megasporogenesis, whereas the hypostase cannot be distinguished until the early proembryonal stages. Consequently, the hypostase cannot, contrary to the views of Ishikawa (1918), play a role in the accumulation of starch grains.

SEED COAT HISTOLOGY (TABLE 6)

Our comparisons are based on mature seeds that no longer contain endosperm, and on those portions of the seed coat that are formed of both inner and outer integuments; descriptions are based on longitudinal sections of mature seeds. In all of the species that we examined, the seed coat had basically the same histological structure, consisting of a two-layered tegmen and a two-layered testa (see Figs. 25–31; Corner, 1976; Eyde, 1978).

As regards the tegmen, all the species had similar cells in the exotegmen and the endotegmen, respectively. The cells of the exotegmen are characteristically elongate and tracheidal, with spiral wall thickenings. In contrast, the cells of the endotegmen are also elongate, but more or less collapsed. Ontogenetically, the cells of the endotegmen become elongate and tanniferous even prior to fertilization (Fig. 24). They may play a role in the early development of the seeds.

In contrast, there was considerable diversity in the structure of the testa, particularly in its thickness, within *Ludwigia*. The cells of the exotesta showed differences in cell substance as well as in size. The exotesta of *L. bonariensis* contained abundant tannins from the early stages of development onward (Figs. 24, 26). In most species, the cells of the exotesta were thin-walled, but those of *L. peploides* were exceptionally lignified and thick-walled (Fig. 31). The endotesta was found to be much more specialized than the exotesta. It was consistently lignified and composed of crystal cells in every species, and varied considerably in thickness from species to species, and from section to section. The endotestae of *L. peruviana* (sect. *Myrtocarpus*; Fig. 25), *L. bonariensis* (sect. *Macrocarpon*; Fig. 26), *L. maritima* (sect. *Ludwigia*; Fig. 27), *L. lanceolata* (sect. *Microcarpium*), *L. leptocarpa* (sect. *Seminuda*; Fig. 30), and *L. peploides* (sect. *Oligospermum*; Fig. 31) had approximately the same thickness throughout an individual seed. The endotestae of *L. repens* (Fig. 29) and *L. arcuata* (sect. *Dantia*) and those of *L. glandulosa* (sect. *Microcarpium*; Fig. 28) differed markedly in that they showed a difference in thickness from part to part: the middle part was thickest (i.e., about 38–44 μm thick), and the portions close to both ends were thinnest (i.e., about 8–17 μm thick).

DISCUSSION

Characteristics of Ludwigia. This study has presented a considerable amount of new embryological data on *Ludwigia* and also critically reviewed the existing literature on the genus. In the light of this information, the embryological characteristics of *Ludwigia* may be summarized as follows:

Anther wall 5- to 6-layered; wall formation conforming to the Basic type; anther epidermis persistent; endothecium fibrous; two to three middle layers ephemeral; tapetum glandular, and its cell 2-nucleate. Cytokinesis in microspore mother cells simultaneous; microspores in a tet-

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Longitudinal section of a three-celled proembryo; apical cell of the two-celled proembryo and its derivatives (ca); basal cell of the two-celled proembryo (cb). Note that the apical cell was divided by a transverse wall. Scale = 10 μm.—20. *L. peploides*. Longitudinal section of a four-celled proembryo showing that the apical cell was divided by a transverse wall, and not by a longitudinal one. Symbols are the same as in 19. Scale = 10 μm.—21 and 22. *L. arcuata*. Longitudinal sections of successively older globular proembryos. Derivatives of the basal cell (cb) at the two-celled proembryo contribute only to a minor part of the embryo and mostly form a short suspensor. Endosperm (e) becomes cellular. Scales = 10 μm.—23. *L. repens*. LS of a mature seed showing a straight dictyledonous embryo (em), which occupies the whole space of the embryo sac. Note that endosperm is absent. Scale = 100 μm.

TABLE 6. A summary of embryological data on seed coat anatomy. Figures for thickness of endotesta in brackets indicate thickness of the thinnest portion of the layer.

	Thickness of Coat Layers				Type of Specialization			
Taxon	Tegmen (number of cell layers)	Testa (number of cell layers)	Endotesta (μm)	Exotesta (μm)	Endo-tegmen	Exotegmen	Endotesta	Exotesta
Sect. *Myrtocarpus*								
L. peruviana	2	2	10.6–12.7	8.5–10.6	none	tracheidal	crystalliferous	none
Sect. *Macrocarpon*								
L. bonariensis	2	2	12.7–14.8	6.3–8.5	none	tracheidal	crystalliferous	none
Sect. *Ludwigia*								
L. maritima	2	2	16.9–21.1	8.5–10.6	none	tracheidal	crystalliferous	none
Sect. *Microcarpium*								
L. lanceolata	2	2	5.3–8.5	8.5–12.7	none	tracheidal	crystalliferous	none
L. glandulosa subsp. *glandulosa*	2	2	38.0–44.4 [14.8–16.9]	14.8–21.1	none	tracheidal	crystalliferous	none
Sect. *Dantia*								
L. repens	2	2	38.0–42.2 [8.5–12.7]	12.7–16.9	none	tracheidal	crystalliferous	none
Sect. *Seminuda*								
L. leptocarpa	2	2	23.2–31.7	19.0–21.1	none	tracheidal	crystalliferous	none
Sect. *Oligospermum*								
L. peploides	2	2 (3)	7.4–10.6	4.2–6.3	none	tracheidal	crystalliferous	none

rahedral, decussate or isobilateral tetrad; pollen grains 2-celled when shed.

Ovule anatropous, crassinucellate and bitegmic; inner integument 2-layered and outer integument also 2-layered, rarely 3-layered (*Ludwigia peploides*); micropyle formed by both integuments.

Archesporium one-celled; archesporial cell cutting off a primary parietal cell and forming a parietal tissue three to six cell layers thick; meiosis in megaspore mother cells resulting usually in a linear tetrad of megaspores, occasionally in a linear triad; micropylar megaspore functional, developing into a 4-nucleate *Oenothera* type embryo sac, comprising an egg, two synergids, and one polar nucleus; apical nucellar epidermal cells not dividing periclinally; prominent accumulation of starch grains in the nucellus common.

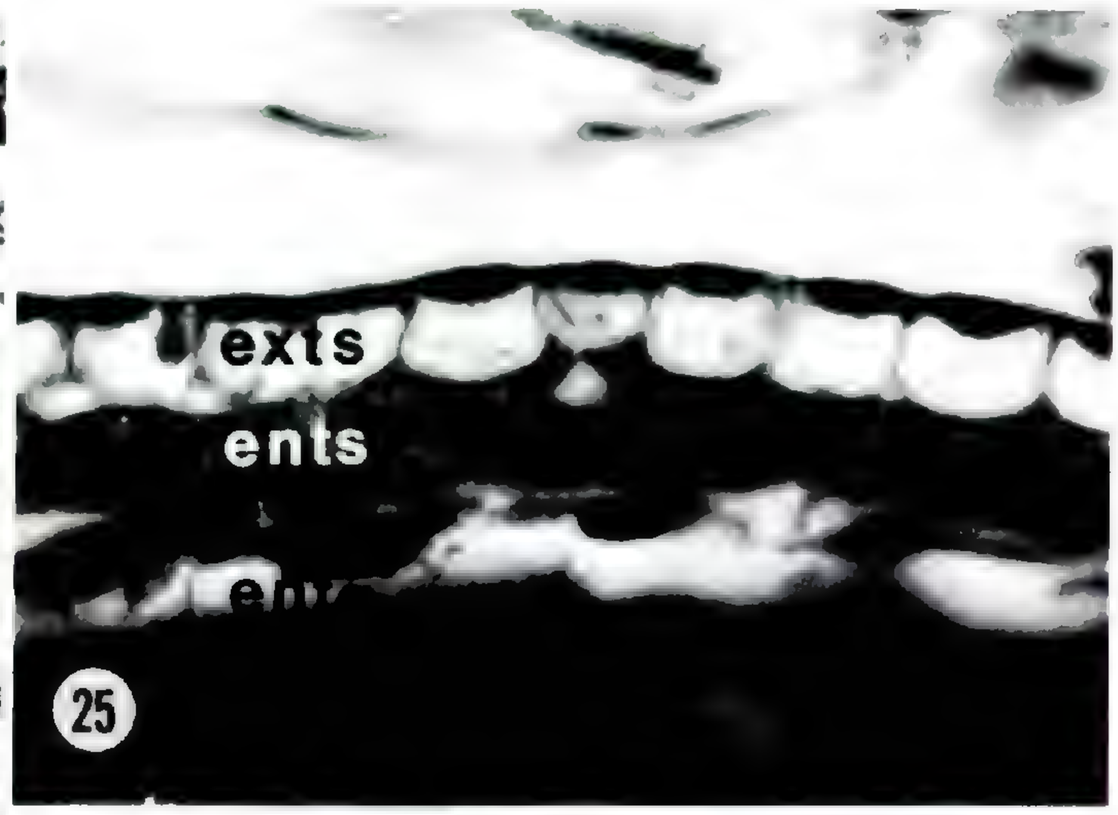
Fertilization porogamous; endosperm formation of the Nuclear type; free-nuclear endosperm becoming cellular later; seed exalbuminous; embryogeny conforming mostly to the Onagrad type, rarely to the Solanad type (*Ludwigia peploides*); suspensor short; embryo straight and with two equally developed cotyledons; hypostase differentiated in proembryonal stages.

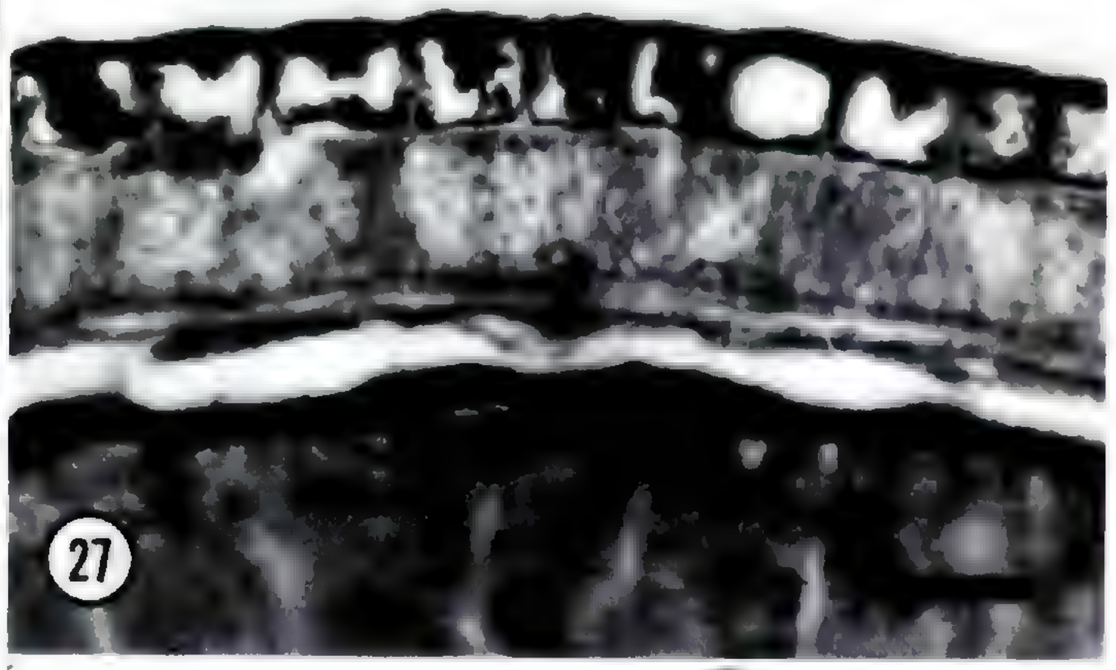
Seed coat composed of 2-layered tegmen and 2-layered testa; exotegmen tracheidal; endotesta crystalliferous, varying in thickness.

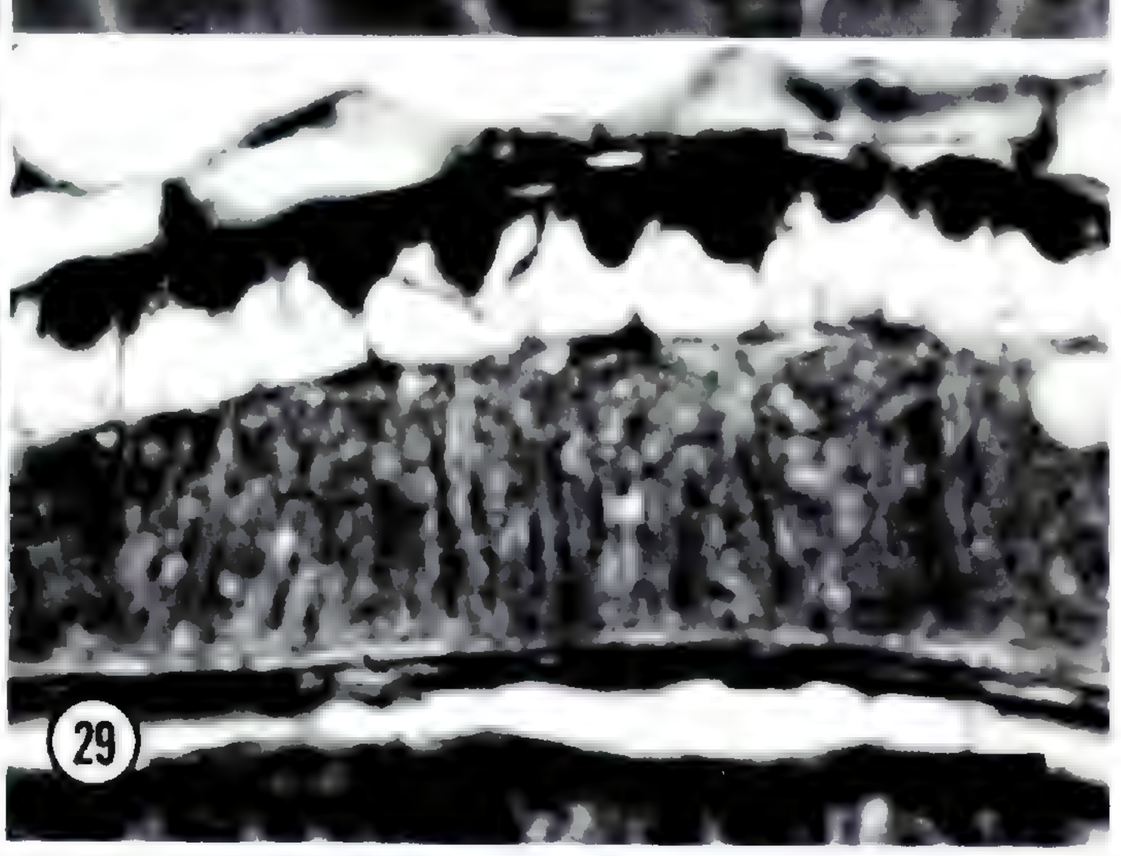
Relationships of sections Microcarpium *and* Dantia. In this discussion, we shall consider only those characteristics that vary within the genus as an index of relationships. As seen in Tables 2–6, however, there are relatively few such characteristics among the embryological features of *Ludwigia*. Furthermore, some of the characteristics that do vary within the genus (e.g., thickness of the anther wall, thickness of the nucellar parietal tissue, thickness of the seed coat, shape of mature embryo sac, and type of embryogeny) do not fall into distinct classes clearly enough to distinguish species or sections from one another. The most diversified and presumably significant character is the histology of the seed coat, which differs from section to section in the degree of specialization of its constituent layers—particularly that of the endotesta.

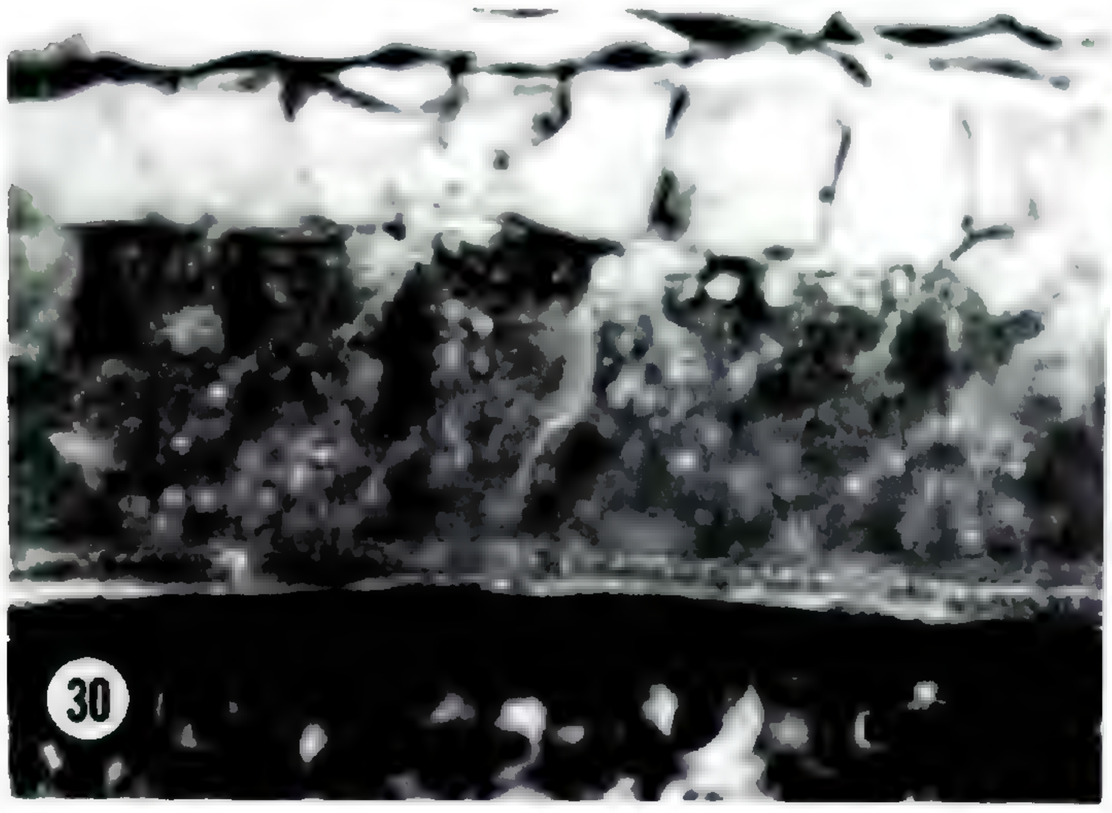
The seed coats of many sections (i.e., *Ludwigia, Macrocarpon, Myrtocarpus, Oligospermum,* and *Seminuda*) exhibit a condition that we regard as generalized; in it, all of the constituent layers are of uniform thickness over the entire seed. We consider structure of this kind to be basic because of its wide distribution in *Ludwigia*. In contrast, sect. *Dantia* exhibits a more specialized structure, in which the endotesta is much thicker at the median part of the seed than at the two ends; the thickest part of the endotesta in species of sect. *Dantia* is as much as 38–44 μm thick (see Table 6). We examined two of the five species of sect. *Dantia,* and Eyde (1978) obtained the same results for a third. In sect. *Microcarpium,* one of the two species examined, *L. lanceolata,* had a seed coat of uniform thickness, whereas another, *L. glandulosa,* had a structure similar to that of sect. *Dantia*. We have checked this character in the other species of sect. *Microcarpium,* and found that some of them (i.e., *L. alata, L. linearis, L. pilosa, L. polycarpa, L. ravenii,* and *L. sphaerocarpa*) have a more or less thin uniform endotesta about 4–16 μm thick, whereas the others (i.e., *L. curtisii, L. linifolia, L. microcarpa, L. simpsonii,* and *L. stricta*) have a thicker endotesta similar to that of sect. *Dantia*.

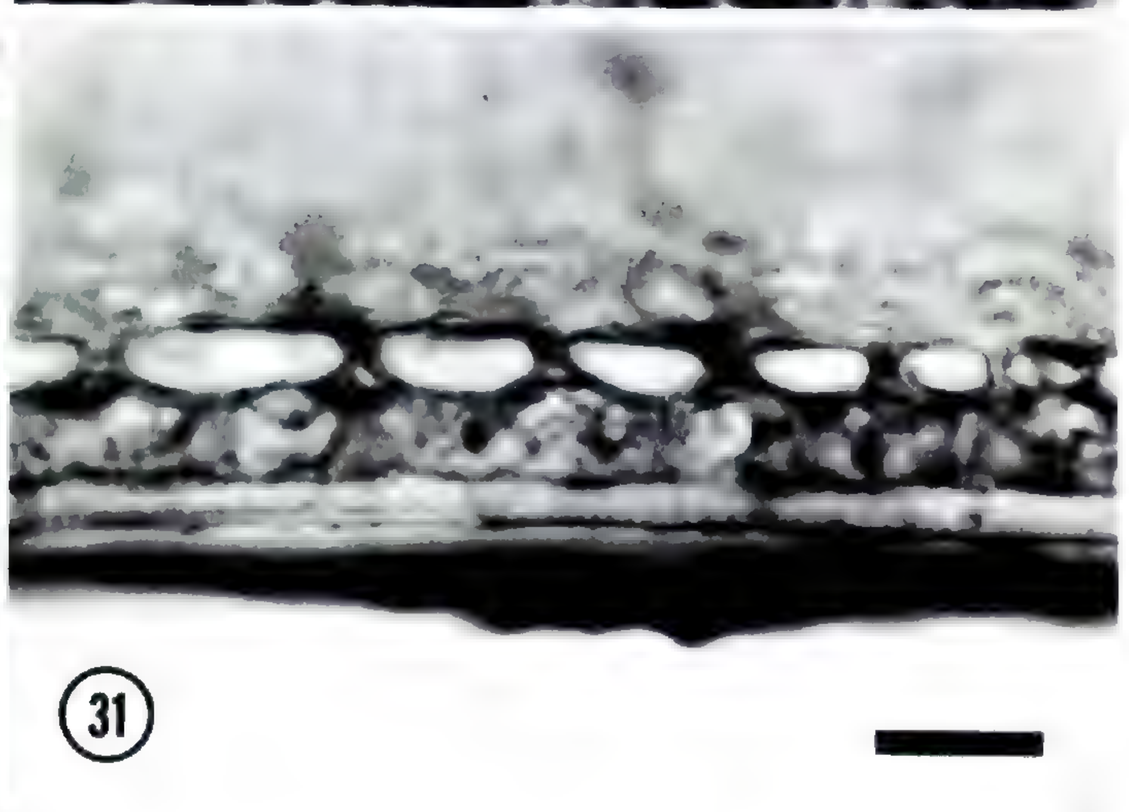
Earlier students, basing their conclusions on other features, pointed out that sect. *Microcarpium* is diverse (see Raven & Tai, 1979). Species differ in seed surface pattern (Eyde, 1978; Peng, 1982), floral vasculature (Eyde, 1981), mode of capsule dehiscence (Peng & Tobe, 1987), histological structure of the capsule wall (Peng & Tobe, 1987), and whether the pollen is shed singly or in tetrads (Raven, 1963). Overall, sects. *Dantia* and *Microcarpium* appear to be closely related (see Raven, 1963; Eyde, 1978, 1981), and hybrids between species of these two sections are easily obtained and fairly frequent in nature (Schmidt, 1967; Peng, 1982). The evidently derived seed coat structure found in six of the 13 species of sect. *Microcarpium* and at least three of the five species of sect. *Dantia* also suggests that these groups are closely related; the kind of specialized seed coat found in these groups is unknown elsewhere in the genus. Eyde (1978: 663) implied that the seed coat structure of these two sections differed, stating that "seeds of sections *Dantia* and *Microcarpium* are histologically similar to those of section *Myrtocarpus,* but in *Ludwigia palustris* (i.e., sect. *Dantia*) the cells of the crystalliferous layer can differ greatly in size from one part of the seed to another, those in the middle of the seed being much larger than those of the ends." We have found, however, that six of the 13 species of sect. *Microcarpium* are identical to sect. *Dantia* in seed coat structure. Different species of sect. *Microcarpium,* although they are clearly related to one another, have both











FIGURES 24–31. Seed coat structure of *Ludwigia*.—24. *L. bonariensis*. Longitudinal section of a young seed showing a tanniferous elongate endotegmen (entg). Scale = 100 μm.—25–31. Longitudinal sections of mature

the generalized and the derived types of seed coat structure, a relationship that makes it almost certain that the specialization of the seed coat structure occurred within this group. Thus by the occurrence in sect. *Dantia* of two synapomorphies—the specialized seed coat and its entirely opposite leaves—that section is clearly derived in the context of *Ludwigia* as a whole.

Relationships with other Onagraceae and Myrtales. In contrast with the traditional view, which holds that *Ludwigia* is the primitive genus closest to the prototype of Onagraceae and therefore the best link with Lythraceae and other Myrtales (see Melchior, 1964; Takhtajan, 1980), recent investigations have made it increasingly clear that *Ludwigia* is, in fact, the sister group of all other Onagraceae (Eyde, 1981: 404; see also Raven & Tai, 1979; Eyde, 1977, 1978). It therefore represents a distinct evolutionary line, but would by no means be expected to have a monopoly on primitive features within the family.

Nonetheless, a comparison of *Ludwigia* with other Onagraceae affords us one important way to evaluate the characteristics of their common ancestor. For example, that *Ludwigia* has the typical distinctive 4-nucleate *Oenothera* type embryo sac like all other Onagraceae clearly indicates that this feature evolved in the ancestor of the family or its derivative before the evolutionary line leading to *Ludwigia* diverged from that leading to the rest of the family.

Earlier embryologists (Tischler, 1917; Mauritzon, 1934; Joshi & Venkateswarlu, 1937) repeatedly suggested that the *Oenothera* type embryo sac might have been derived from the normal-type embryo sac of Lythraceae, which like *Oenothera* lacked antipodal cells at maturity because they were ephemeral. We now know, however, that ephemeral antipodal cells are characteristic of most Myrtales and do not, therefore, support a hypothesis of a direct relationship between Onagraceae and Lythraceae (Tobe & Raven, 1983); moreover, the lack of antipodal cells in mature embryo sacs has a completely different basis in Onagraceae, where they are never formed, from that in other Myrtales, where they are formed and then lost. The comparison is a false one, based on superficial convergence.

The *Oenothera* type embryo sac is quite different from the normal-type embryo sacs in the following two respects: (1) the micropylar megaspore in a tetrad, instead of the chalazal one in the case of the normal type, always functions to develop into an embryo sac; (2) the nucleus of the functional megaspore always divides twice, instead of three times, which results in a 4-nucleate embryo sac. With respect to a reversed polarity of the functional megaspore, Rodkiewicz and Bednara (1974) have postulated that the uneven distribution of starch grains and dictyosomes in megaspores as well as of callose on megaspore walls may prevent the development of the chalazal megaspore into an embryo sac. Starch grains accumulate in the micropylar megaspore but not to as great an extent as in the chalazal one; dictyosomes occur at a greater density in the chalazal megaspore than in the micropylar one; and callose is laid down on all megaspore walls except for the upper wall of the micropylar megaspore.

The kind of embryo sac that is characteristic of Onagraceae, which has only four nuclei, might be regarded as a result of neoteny: functioning at an earlier stage of development than is characteristic of most plants. The several substantial differences between the *Oenothera* type of embryo sac and that characteristic of most angiosperms suggest that the former may have originated as a result of the accumulation of several different mutations. It is probably because of the complex nature of these differences that the *Oenothera* type embryo sac is unknown except in Onagraceae. Judged from its ubiquity in the family, this unique type of embryo sac must have been present in the common ancestor of the two fundamentally different lines leading, respectively, to *Ludwigia* and to the rest of the family.

Onagraceae resemble Lythraceae in a number of features, including wood anatomy (Carlquist, 1975), leaf architecture (Hickey, pers. comm., in Dahlgren & Thorne, 1984), seed coat histology (Corner, 1976), and petal venation pattern (Chrtek, 1969). Our results confirm that these two families share a specialized tracheidal exotegmen, which, however, is also found in two unrelated families of Myrtales; i.e., Combreta-

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seed coats, each of which is composed of a two-layered testa and a two-layered tegmen; exotesta (exts); endotesta (ents); exotegmen (extg); endotegmen (entg). Scales = 20 μm.—25. *L. peruviana.*—26. *L. bonariensis.*—27. *L. maritima.*—28. *L. glandulosa.*—29. *L. repens.*—30. *L. leptocarpa.*—31. *L. peploides.*

ceae and Trapaceae (Corner, 1976). In Myrtales generally, starch grains accumulate in the nucellus only in Onagraceae and Lythraceae. Ishikawa (1918) reported abundant starch grains in *Oenothera, Gaura,* and *Circaea* (Onagraceae), and Hubert (1896) in *Cuphea* (Lythraceae). We here report their ubiquitous occurrence in *Ludwigia* as well.

We are at present studying the embryology of all other 16 genera of Onagraceae as well as of some Lythraceae. Further detailed comparisons will be presented in subsequent papers.

Embryology and relationships within Ludwigia. Many past studies of embryology have been too limited in scope to warrant the general conclusions that have been drawn from them. Most have been concerned only with the development of the male and female gametophyte and that of the embryo, and the number of actual observations made have often been too few to warrant the generalizations that have been based on them. Our present study has been based on a sufficient number of species to represent the range of variation of the genus and has included, insofar as possible, all of its embryological features. In the light of this information, it is possible to offer some suggestions about relationships within *Ludwigia,* based on our observations.

Most embryological features in *Ludwigia* did not vary throughout the genus. However, differences in two important features have been noted within the genus, and these are the type of embryogeny and the structure of the endotesta. Along with earlier students of *Ludwigia* embryology, we found that most species we examined had the Onagrad type embryogeny. The only exception was *L. peploides* (sect. *Oligospermum*), which had the Solanad type embryogeny. This finding agrees with other evidence in suggesting an isolated position for sect. *Oligospermum* within the genus, although the earlier report of Onagrad type embryogeny in *L. adscendens* (= "*Jussieua repens*"; Khan, 1942), a species that is very closely related to *L. peploides,* needs to be investigated. Embryogeny often varies considerably at a family level (see Davis, 1966: 25–26), and a sufficient number of species need to be investigated before conclusions are drawn about this feature.

As we mentioned above, the species of *Ludwigia* sect. *Dantia* and some species of sect. *Microcarpium* have a more specialized endotestal structure than the rest of sect. *Microcarpium* and the other species of the genus. Based on the occurrence of this clearly apomorphic feature, it seems certain not only that the groups are directly related, but that sect. *Dantia,* with its opposite leaves—another clearly apomorphic feature, unique for *Ludwigia*—was derived from an ancestor that would, if it were known, be placed in sect. *Microcarpium.* Although diverse, sect. *Microcarpium* seems clearly to consist of elements that are directly related to one another.

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KOEHNERIA, A NEW GENUS OF LYTHRACEAE FROM MADAGASCAR[1]

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ABSTRACT

The new monotypic genus *Koehneria* is described, based on *Pemphis madagascariensis*, one of two species of the lythraceous genus *Pemphis*. It is distinguished from *Pemphis acidula* and other members of the Lythraceae by a combination of characters including: glandular trichomes, strongly reflexed calyx lobes, doubled episepalous stamens, a conspicuous ovary stipe, elongated inner epidermal cells of the ovary wall, septifragal capsule dehiscence, 3-pseudocolpate pollen, and wood with septate fibers, scanty parenchyma, and erect ray cells. Morphological, palynological, and anatomical comparison of *Koehneria* is made to the Old World genera *Pemphis, Lagerstroemia, Woodfordia*, and the New World genera *Adenaria* and *Pehria*. The last three genera share with *Koehneria* a three-character synapomorphy absent from *Pemphis* and *Lagerstroemia* and all other genera of the family. A common ancestral origin is postulated for *Koehneria, Woodfordia, Adenaria*, and *Pehria*, but subsequent extensive morphological divergence, together with wide geographic dispersal and extinction of intervening forms, limits understanding of more specific inter-generic relationships.

Among the 15 monotypic or ditypic genera of the family Lythraceae is the Old World genus *Pemphis*, whose two species have long been regarded as highly disparate (Koehne, 1901). *Pemphis acidula* Forster, the type of the genus, is a well-known, widely-distributed species of strand and dune habitats occurring on the east African coast and eastward on islands throughout the Indian and western Pacific Oceans. *Pemphis madagascariensis* (Baker) Koehne, in contrast, is an endemic of semiarid savannahs of the southern half of Madagascar. Recently, new collections of *P. madagascariensis* became available for study, allowing the question of the species' generic status and its affinities to other members of the family to be reassessed from a more extensive data base.

Pemphis madagascariensis was originally described as a *Lagerstroemia* from south-central Madagascar in 1881 (Baker, 1881, 1882). At that time, only flowering material, without fruits, was known. Koehne's monograph of *Lagerstroemia*, which followed soon after, included the species, although it was noted that authentic material had not been seen by the author (Koehne, 1883). In 1896, a second species of *Pemphis, P. punctata* Drake, was described from the same general geographical area as *L. madagascariensis* and was distinguished from *P. acidula* by the presence of punctae on the leaves, buds, and ovaries and by the long-exserted stamens and style. Koehne, in monographing the family Lythraceae, remarked that he had yet to see a single flower of *Lagerstroemia madagascariensis* (18 years after his treatment of *Lagerstroemia*) and noted in the same work that *P. punctata* was quite different from *P. acidula* although they shared the same inflorescence type (Koehne, 1901). In completing the monograph of the Lythraceae, Koehne finally was able to study material of this taxon from Kew, which included important features of the seed, undescribed until then, and as a result he transferred *Lagerstroemia madagascariensis* to *Pemphis*, citing *P. punctata* in synonymy (Koehne, 1903).

The generic position of *Pemphis madagascariensis* has depended exclusively on inflorescence and floral morphological features observed at the turn of the century. This study presents detailed floral morphological and anatomical features, leaf

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and wood anatomical characteristics, and pollen morphology for *P. madagascariensis,* and provides comparison to *P. acidula* and other putative allies. The unique circumscription of *P. madagascariensis* described here supports its treatment as a new genus of the Lythraceae.

Materials and Methods

Observations on floral and seed morphology and floral anatomy of *Pemphis madagascariensis* were based on FAA-preserved material (*D'Arcy & Rakotozafy 15317,* MO; *Dorr et al. 3923, 3933,* MO), supplemented by dry materials from herbarium specimens (TAN and MO). Anatomical observations of flowers were made using microtome sections prepared following a standard paraffin method; scanning electron-microscopic observations were made according to standard techniques using a JSM-25S (JEOL) microscope.

The following additional fixed materials were compared: *Adenaria floribunda* H.B.K., *Knapp & Schmalzel 5208* (MO); *Pehria compacta* (Rusby) Sprague, *Berry 4006, 4028* (VEN); *Pemphis acidula* Forster, *Raulerson s.n. in 1982* (MO); *Woodfordia fruticosa* Kurz, *Dice & Musial s.n. in 1983* (MO), *Nasir s.n. in 1983* (MO), and *Bird s.n. in 1983* (MO).

For leaf anatomical descriptions of *Pemphis madagascariensis,* material of *R. Decary 8940* (L) and *L. Bernardi 11181* (L) was studied. For leaf-anatomical comparisons, data scattered in the literature and summarized by Solereder (1899, 1908), Metcalfe and Chalk (1950) and Napp-Zinn (1973, 1974) were complemented with original observations for *Adenaria, Pehria, Lagerstroemia,* and *Woodfordia* in order to contribute to an assessment of the affinities of this new genus. Sections of other genera represented in the Rijksherbarium slide collection (*Ginoria, Lawsonia, Lafoensia,* and *Physocalymma*) were also included in the comparison. For wood anatomy, twigs of *P. madagascariensis* 3 and 4.5 mm in diameter were studied from the collection *D'Arcy & Rakotozafy 15317* (MO) and ca. 12 mm diameter from *Dorr et al. 3923, 3933* (MO). The paper by Baas and Zweypfenning (1979) served as a source of comparative data, complemented by sections of twig material of *Pemphis* and *Lagerstroemia.*

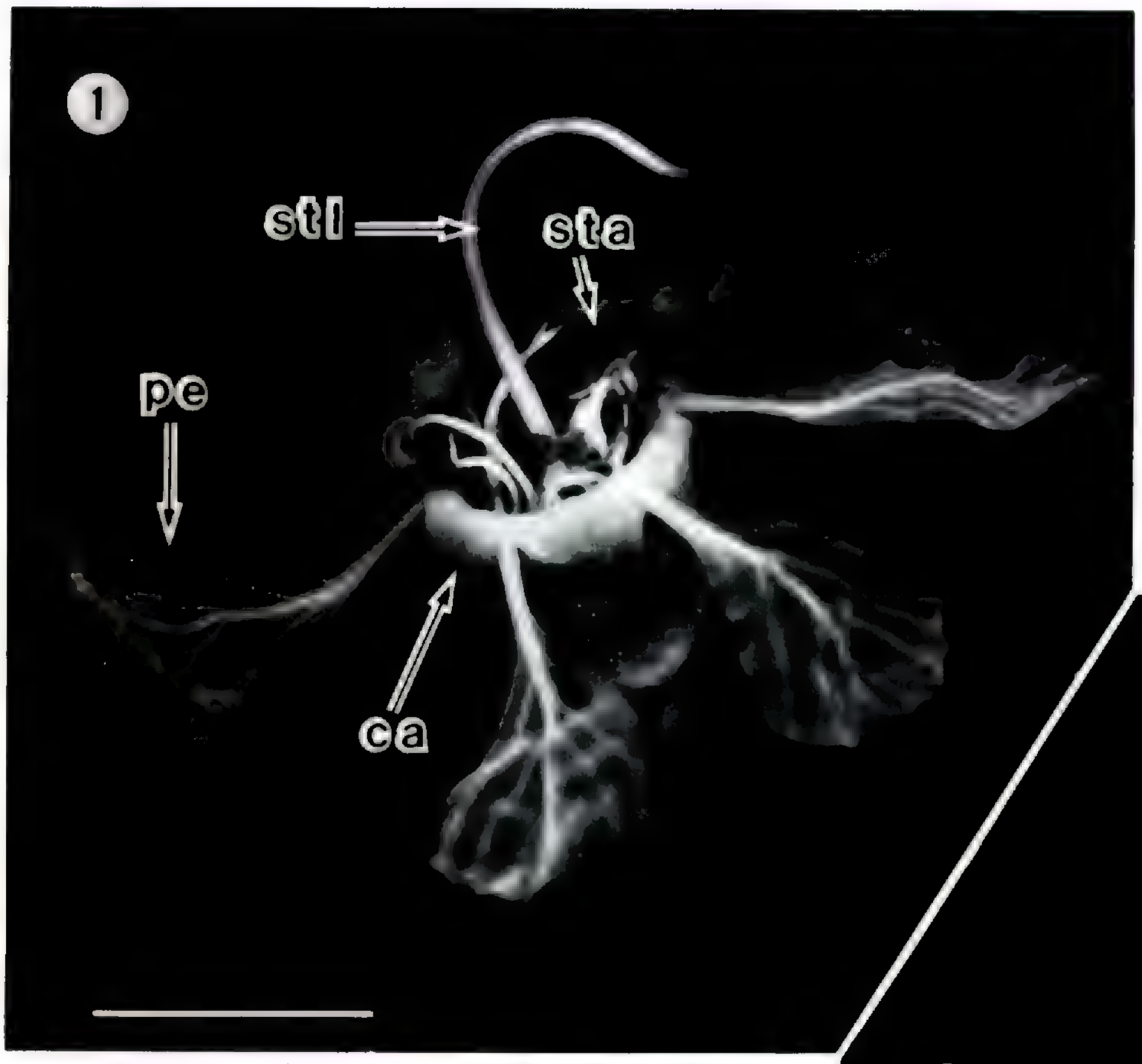
Light microscope and scanning electron microscope (SEM) comparisons of pollen of *Pemphis madagascariensis* were made with pollen of all genera of the Lythraceae utilizing the pollen collections of A. Graham, Kent State University. A Cambridge Stereoscan SEM 100 was employed for pollen and leaf trichome photos.

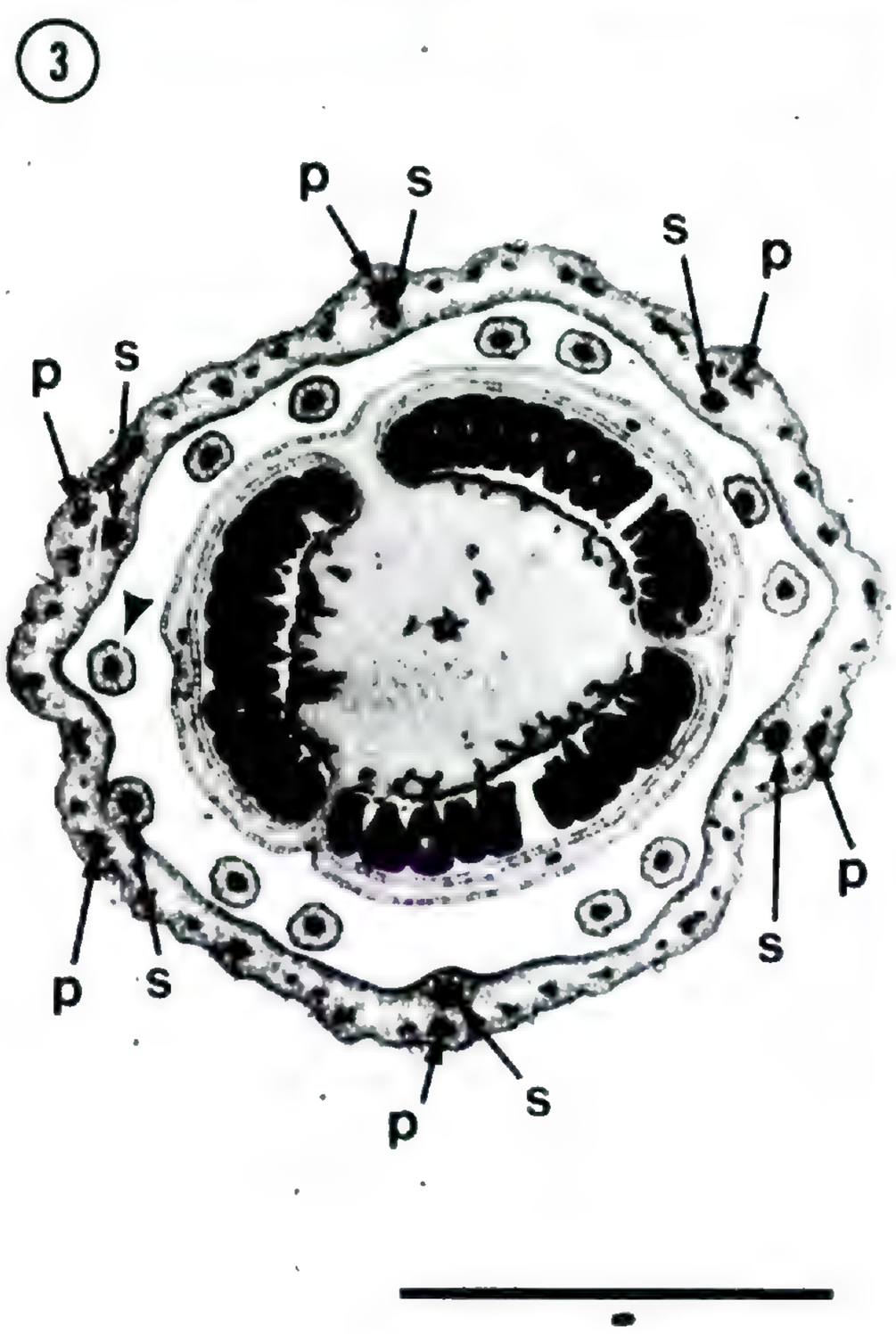
Floral Morphology

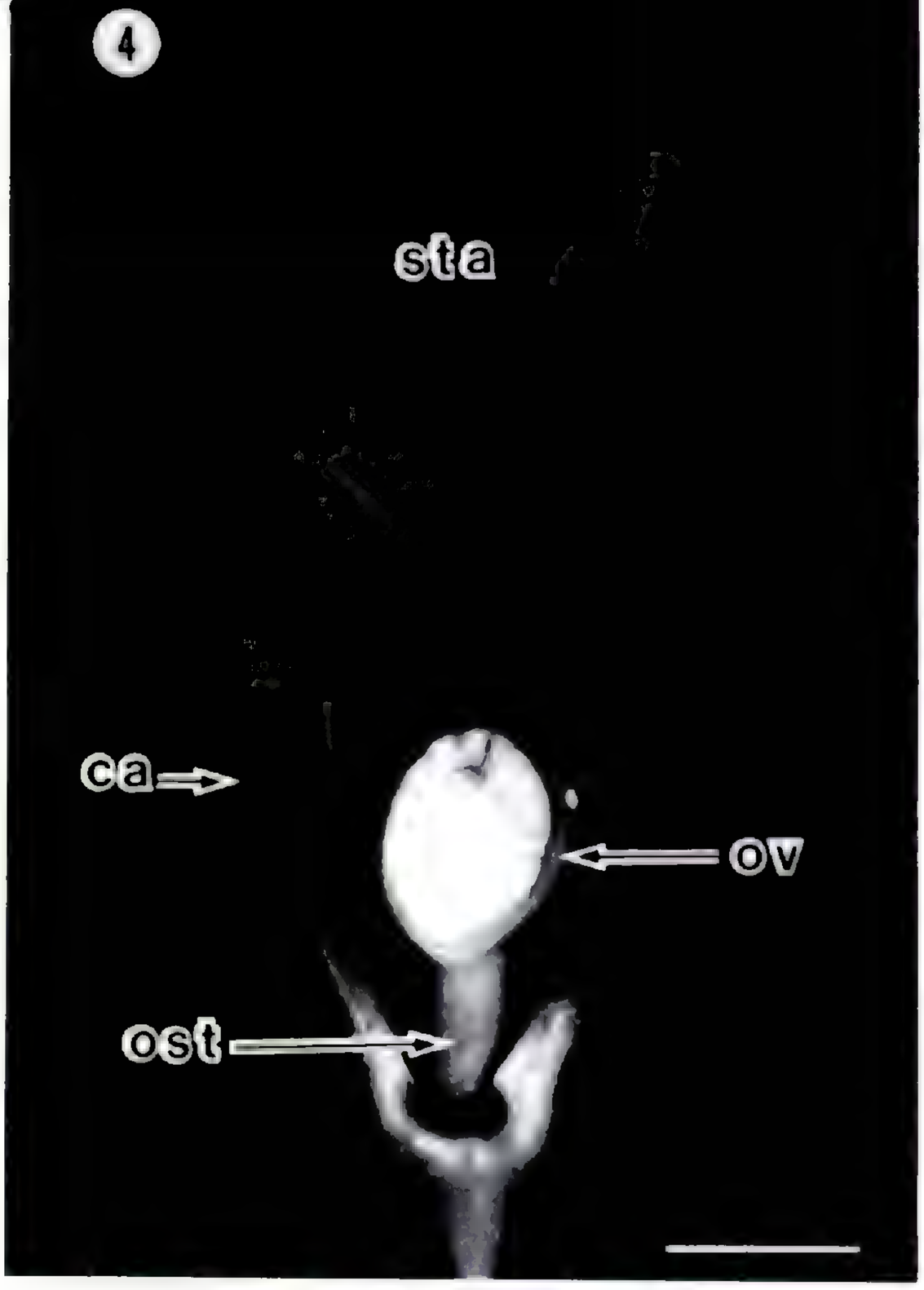
Flowers are homomorphic, actinomorphic, perfect, and basically 6-merous (Fig. 1). The floral tube is campanulate, and the length from the base to the tip of the calyx lobes is 4.5–8.5 mm. The calyx lobes are six in number, deltoid, and strongly reflexed (Figs. 1, 4). A conspicuous appendage (the epicalyx) is present at the sinus between adjacent lobes and its length varies from 0.0 to 2.0 mm. There are six petals opposite the appendages. These are widely obovate with a short claw, 5.5–10.0 mm long and 4.0–7 mm wide (Fig. 2). The venation of the petals is simple, with a thick midvein present in the center, and four or five secondary veins. There are no anastomoses between the secondary veins (Fig. 2).

The androecial position is perigynous. The stamens are commonly 18 in number (occasionally fewer or more) of which 12 (10–14) are opposite the sepals, and 6 opposite the petals. Episepalous stamens are inserted at nearly two-fifths the height of the floral tube, and epipetalous stamens at a slightly higher level (Fig. 3). The episepalous stamens are generally paired; in Figure 3 ten of the 11 episepalous stamens are paired, the single remaining one is indicated by an arrow. The paired stamens seem to have been derived by early splitting of the stamen meristem (chorisis), an occurrence common in several Lythraceous genera such as *Lagerstroemia, Crenea, Lawsonia, Nesaea, Heimia,* and *Ginoria* (Tobe et al., in prep.). Rarely, additional stamens are produced by splitting of a filament 1–2 mm above the point of insertion to form two stamens. Filaments of the episepalous stamens are 10–11 mm long, somewhat longer than those of the epipetalous stamens, which are 7–8 mm long. Exsertion of episepalous and epipetalous stamens approximately equals the length of the floral tube (Fig. 4).

The ovary is superior and globose, with a conspicuous stipe, 1.0–1.2 mm long (Figs. 4, 7). Presence of a comparable ovary stipe is seen elsewhere in the family only in *Adenaria* and *Pehria.* The style is narrow, slightly exceeding the stamens, and 7–15 mm long. It tapers to a punctiform stigma. The capsule is globose, and the mode of dehiscence is probably septifragal marginicidal. Although sometimes incomplete, dehiscence occurs from the top of the capsule by







FIGURES 1–4. *Koehneria madagascariensis*.—1. Flower.—2. Petal cleared with 8% KOH.—3. Transverse section (TS) of flower. Note that, while TSs of filaments of episepalous stamens appear as paired small circles, TSs of filaments of epipetalous stamens do not appear yet at this level. An arrow indicates a non-paired, single episepalous stamen.—4. Lateral view of dissected flower. Abbreviations: ca, calyx lobe; pe, petal; sta, stamen; stl, style; p, vascular bundle to a petal; s, vascular bundle to a stamen; ost, ovary stipe; ov, ovary. Scale equals 5 mm for Figure 1; 1 mm for Figure 2; 2 mm for Figures 3 and 4.

two or three longitudinal lines along the ovary septa to approximately half the length of the capsule. The seeds are more or less conical with the chalazal part broadest (Fig. 9). They are small, 1.2–1.3 mm long and 0.9–1.0 mm wide. The seed coat surface is almost smooth, without specializations such as the inverted epidermal hairs found in a number of lythraceous genera.

Floral Anatomy

In anatomical section nectariferous tissue may be seen forming a narrow ring at the base of the floral tube surrounding the ovary (Fig. 7). Cells of the tissue are densely cytoplasmic, making the tissue easily recognizable in thin section because of its high stainability.

The number of locules (or constituent carpels) of the ovary is often three (Fig. 3), not always two as has been described (Koehne, 1903). The ovary wall is thin and four to five cells thick with inner epidermal cells of the wall showing remarkable radial enlargement (Fig. 8).

Trichomes

Two types of trichomes occur in the species, one a simple unicellular falcate hair, the other multicellular, globose, and glandular. The unicellular hairs form a very dense cover on the abaxial leaf surface (Fig. 12) and a sparser one on the adaxial side. Glands are also more abundant and larger on the abaxial than on the adaxial surface. Both types are abundant on leaves, young branches, pedicels, and the outer surface of the floral tube (Figs. 5, 6, 12). Both types also occur on the upper half of the ovary, although the glandular hairs are most abundant (Fig. 6; see also Fig. 8). Unicellular trichomes are 90–180 μm long; glandular trichomes are 70–130 μm in diameter. There is no size difference between glandular trichomes on the flower surface and those on the ovary surface.

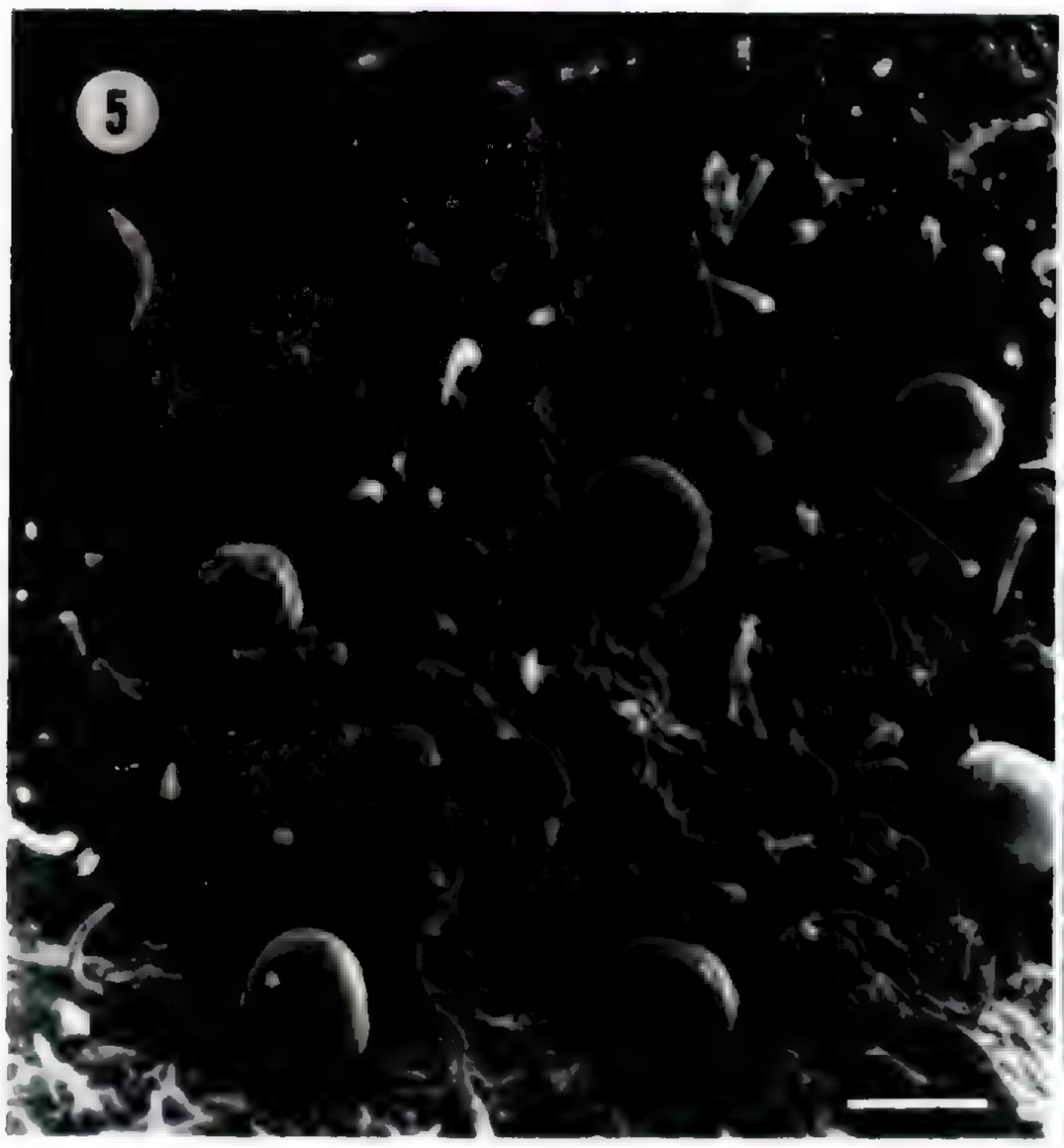
Leaf Anatomy

In surface view the leaves have an indumentum of unicellular hairs and globular, multicellular glands (dark dots as seen with a hand lens) (Figs. 12, 13). The unicellular hairs are proximally broad and slender and thick-walled distally (Fig. 14). The glands on the abaxial surface are 100–130 μm in diameter, on the adaxial surface 70–90 μm. They are sessile, with a very short multiseriate base, and composed of one (locally two) layers of cells enclosing a large cavity with more or less granular contents (Fig. 15; the structure of mature glands suggests a lysigenous or schizolysigenous development of these cavities). Epidermal cells have straight to curved anticlinal walls. Stomata are confined to the abaxial surface, anomocytic to cyclocytic, and the guard cell pairs are (18–)20(–22) μm wide, (22–)24(–26) μm long.

In transversal section the lamina is dorsiventral, ca. 170–200 μm thick; the cuticle is 1 μm thick or less. Epidermal cells are almost all with convex periclinal walls and mucilaginous, although sometimes with periclinal division walls and then only the inner daughter cell mucilaginous. The stomata are slightly raised but well protected by dense hair cover; inner and outer cuticular ledges are fairly well developed. A hypodermis is absent. The mesophyll is composed of one layer of tall palisade cells and spongy tissue. The midrib is provided with a single, bicollateral vascular bundle, linked through a collenchymatous bundle sheath extension to the upper epidermis and by a parenchymatous to collenchymatous ground tissue to the lower epidermis, without supporting sclerenchyma. Minor veins are mostly embedded in the mesophyll; vascular bundles of the major lateral veins are vertically transcurrent through parenchymatous to collenchymatous bundle sheath extensions. Crystals are present as druses in the vicinity of vascular bundles.

Wood Anatomy

Growth rings are faint to distinct. Vessels are diffuse or wood is semi-ring-porous in some of the growth increments. Vessels number ca. 150–200 per sq. mm, ca. 25–45% are solitary, the remainder in radial multiples of 2–4(–7) or more rarely in small clusters, round to oval, the tangential diam. (20–)40(–60) μm, the radial diam. up to 70 μm, the walls 3–4 μm thick. Vessel member length is (180–)360(–420) μm. Perforations are simple in oblique to nearly horizontal end walls. Inter-vessel pits are crowded, alternate, vestured, round to polygonal, 3–5 μm, with slit-like apertures. Vessel-ray pits are similar but half-bordered. The fibers are (370–)580(–770) μm long, with walls medium to very thick, sometimes weakly gelatinous, with simple to minutely bordered pits confined to the radial walls, septate. Parenchyma was not seen. Rays are mainly uniseriate, partly with low biseriate portions, al-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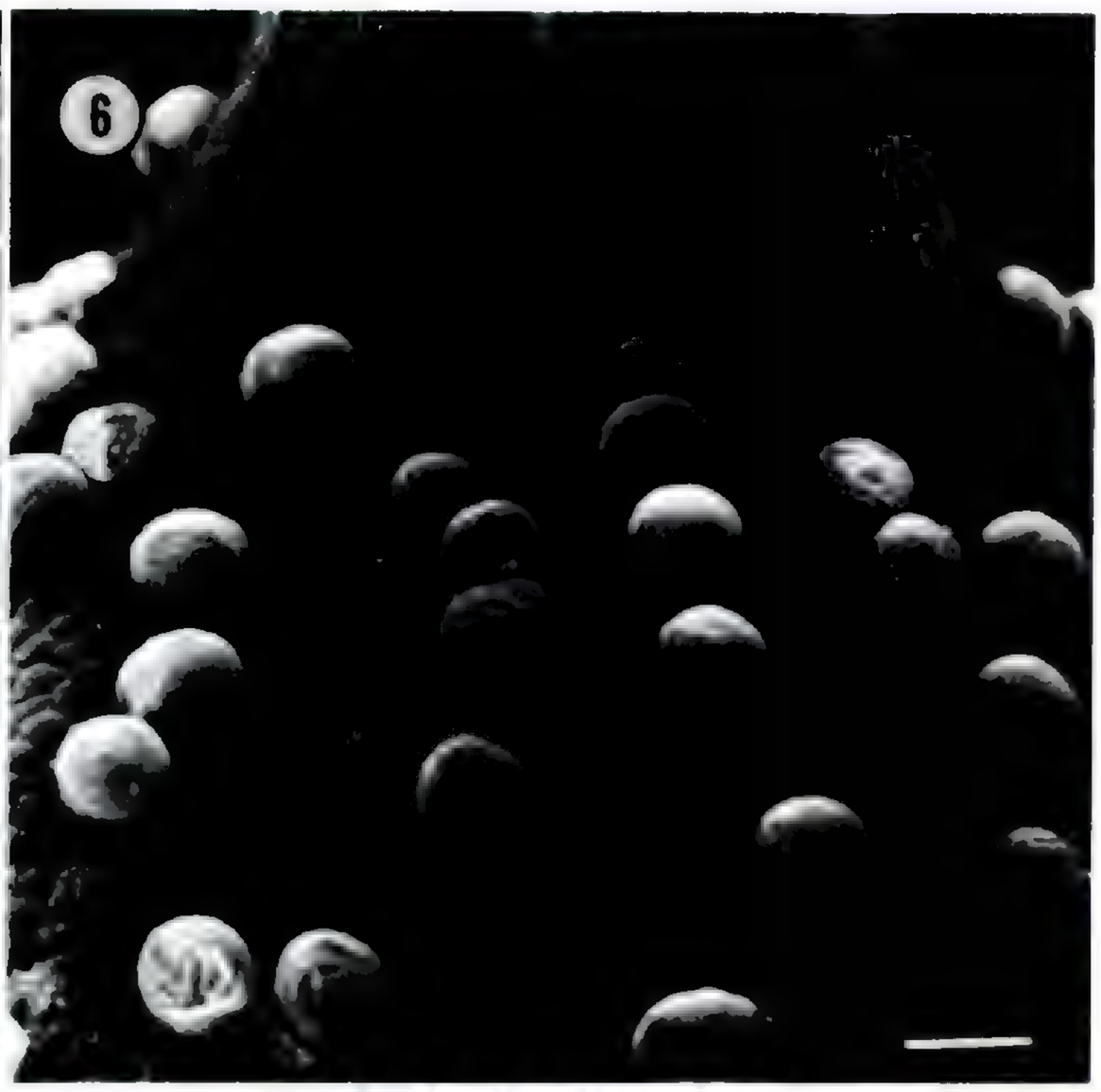
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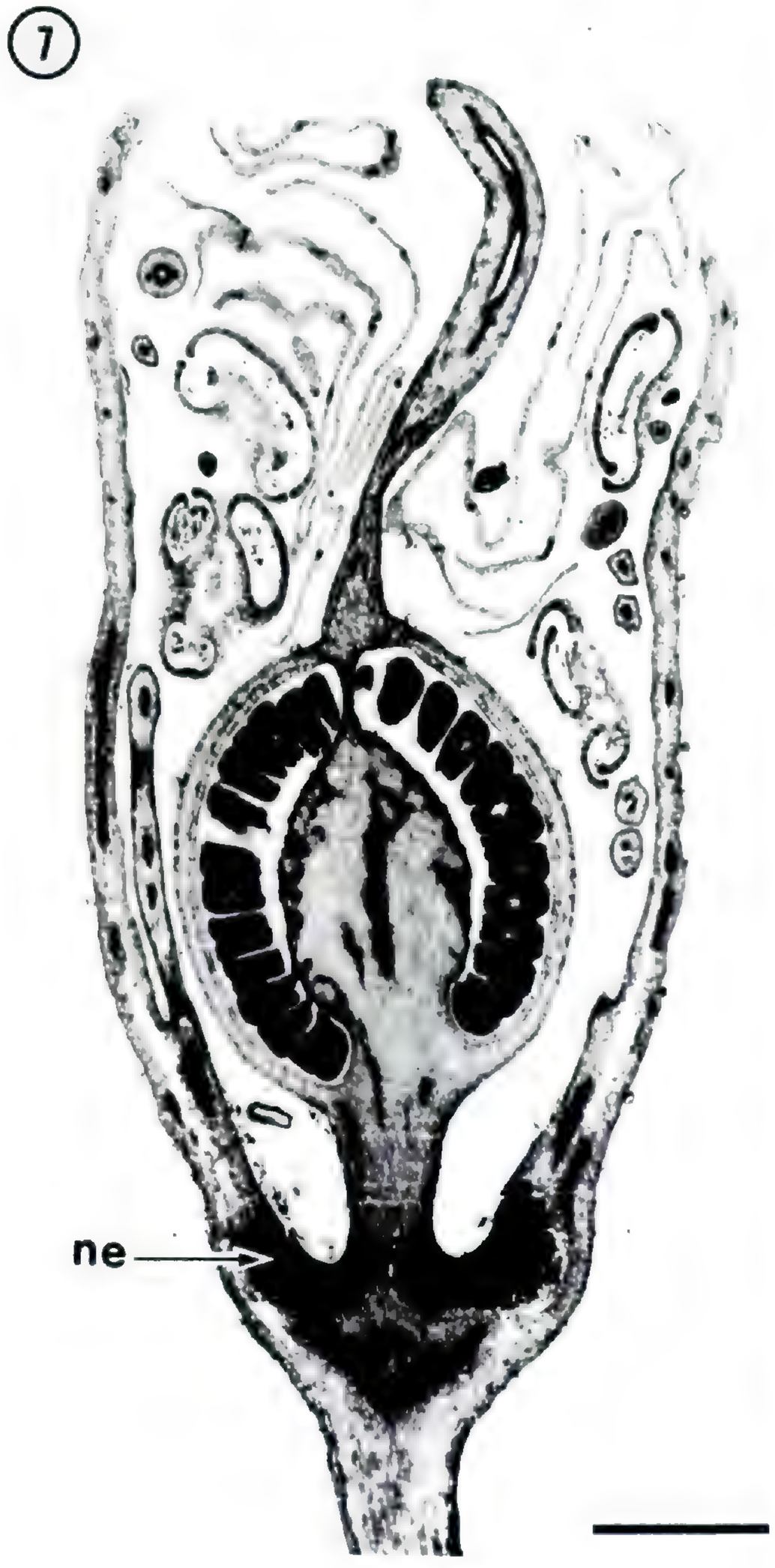
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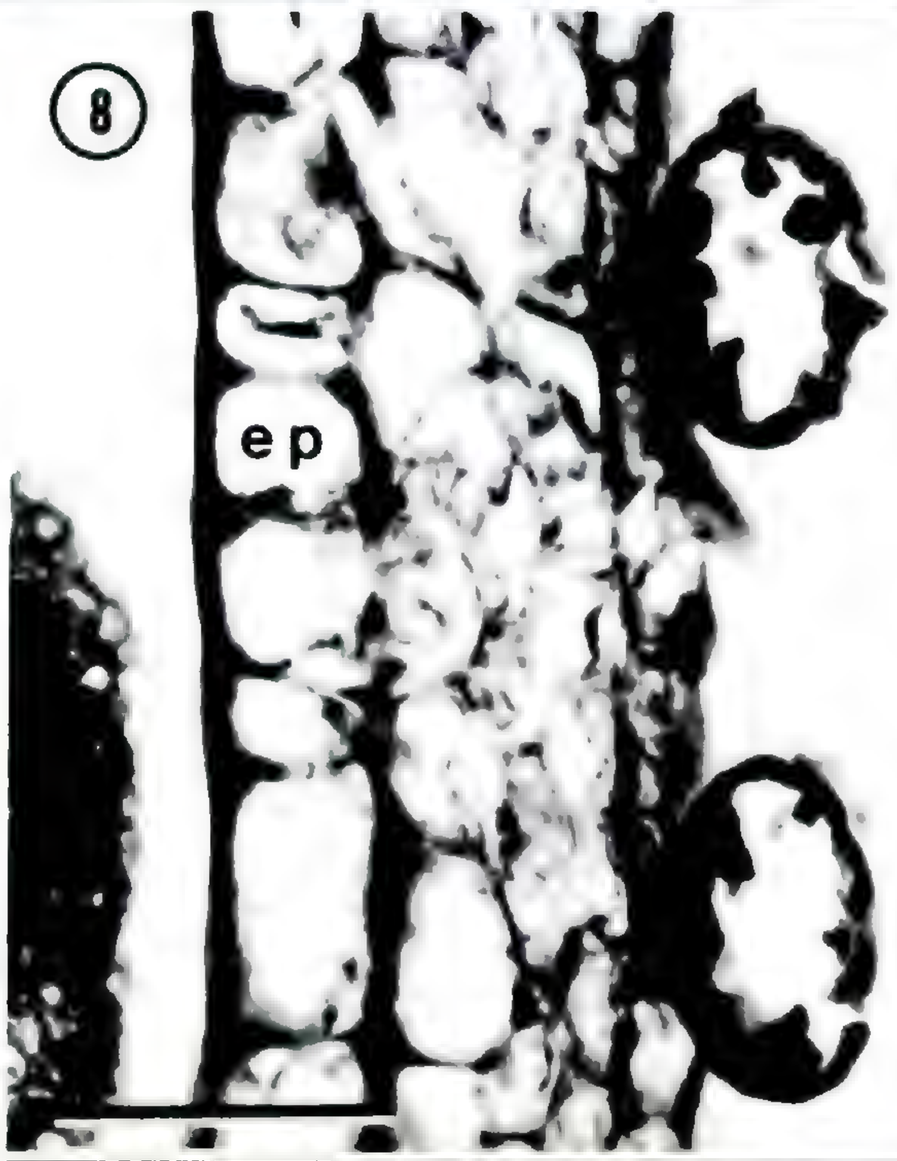
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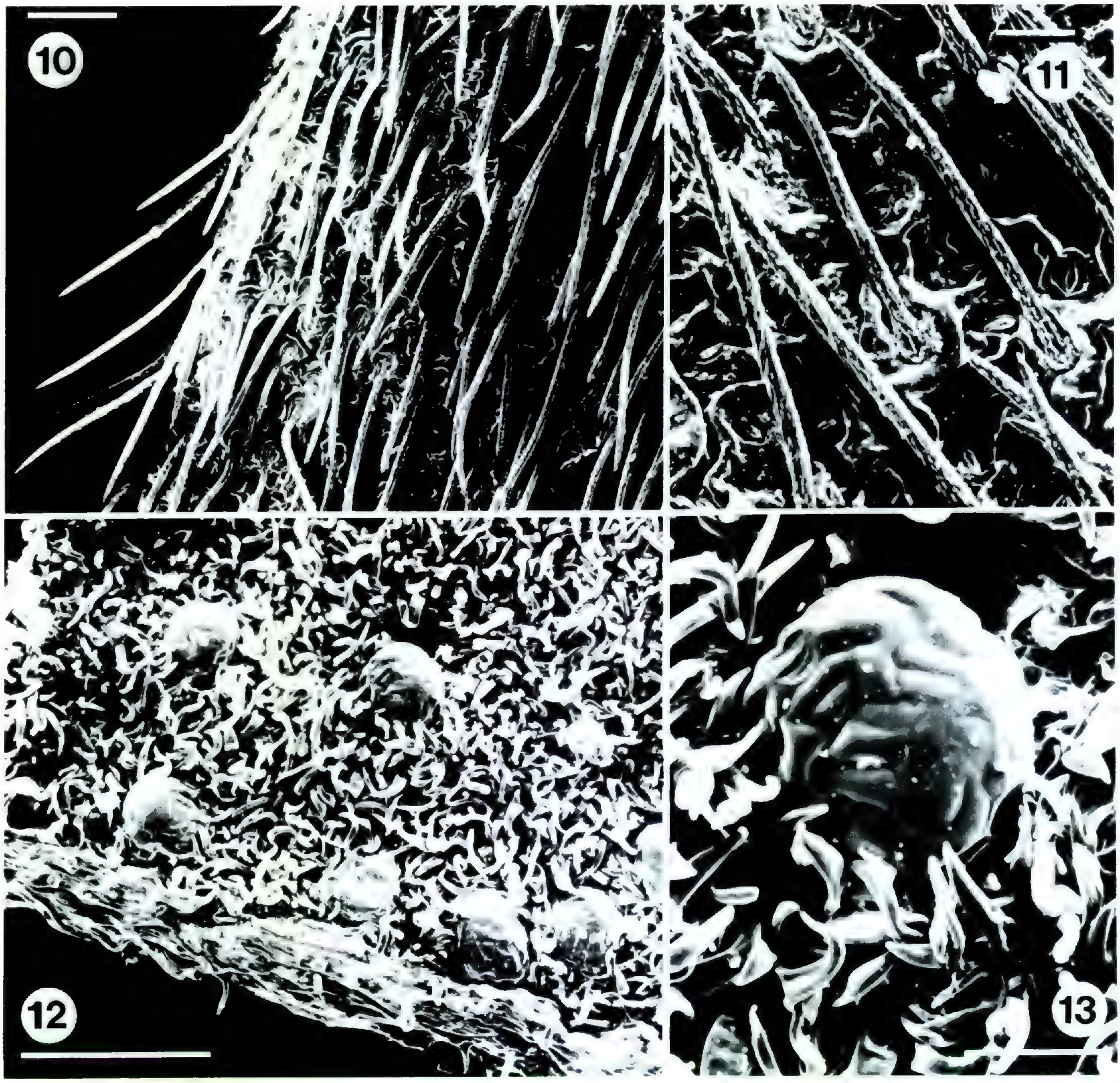

FIGURES 10–13. Scanning electron micrographs of lower leaf surfaces of *Pemphis acidula* [*Cramer 4935* (MO)] and *Koehneria madagascariensis* [*D'Arcy & Rakotozafy 15317* (MO)].—10. Seriaceous lower leaf surface of *P. acidula*.—11. Enlargement of unicellular trichomes of *P. acidula*.—12. Tomentose lower leaf surface of *K. madagascariensis*.—13. Enlargement of multicellular, globose, glandular trichome, surrounded by unicellular, non-glandular trichomes of *K. madagascariensis*. Scale equals 200 μm for Figures 10 and 12; 50 μm for Figures 11 and 13.

most entirely composed of upright cells, central cells sometimes square to weakly procumbent (this ray type would probably develop into heterogeneous type I in a more mature stem). Crystals were not observed. Many fibers with dark-staining contents (probably living fibers) are present (Figs. 16, 17).

Additional stem characters are: Phloem de-

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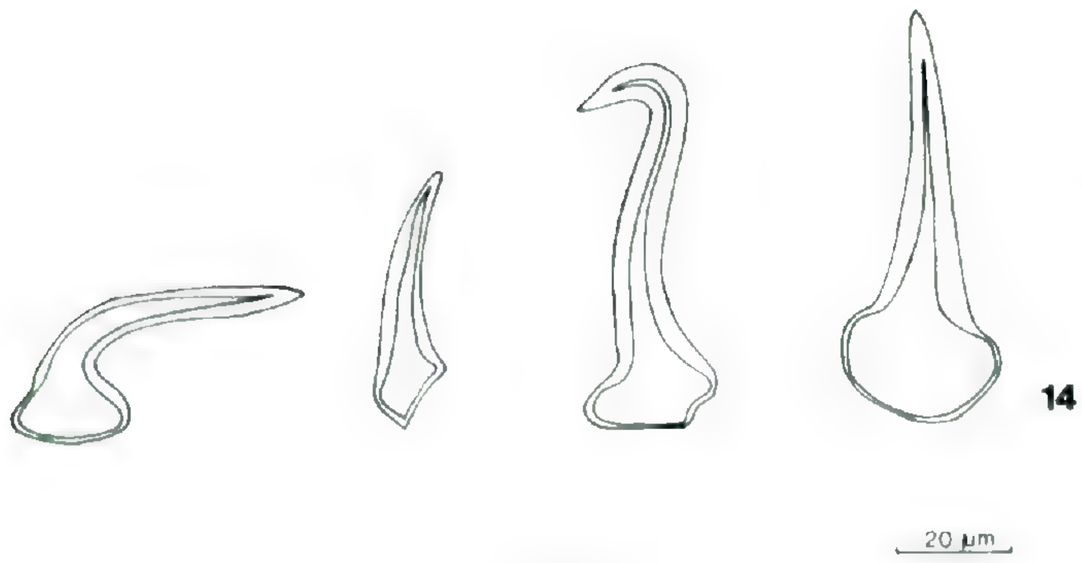
FIGURES 5–9. *Koehneria madagascariensis*.—5. Scanning electron micrograph of trichomes on the outer surface of the floral tube.—6. Scanning electron micrograph of trichomes on the surface of the upper half of the ovary.—7. Longitudinal section (LS) of flower.—8. LS of ovary wall.—9. Scanning electron micrograph of nearly mature seed [see specimens examined, *Réserves Naturelles 2689* (TAN)]. Abbreviations: ne, nectariferous tissue; ep, inner epidermal cell. Scale equals 100 μm for Figures 5, 6, 8, and 9; 1 mm for Figure 7.



FIGURES 14, 15. Camera lucida drawings of leaf trichomes of *Koehneria madagascariensis*.—14. Unicellular trichomes; three trichomes on the left from lower epidermis and one on the right from upper epidermis.—15. Multicellular, glandular trichome from lower leaf surface. Scale equals 20 µm.

void of sclerenchymatous elements; secondary phloem with narrow bands of crystalliferous cells containing druses; interxylary phloem well-developed; pith with nests of thick-walled sclereids.

POLLEN MORPHOLOGY

The pollen is prolate-spheroidal and tricolporate with three faint pseudocolpi (Figs. 18–20, 24). The colpi are meridionally elongated, equatorially arranged, equidistant, straight, 10–16 µm long, extending to within 3 µm of the pole and tapering to an acute apex; costae colpi are narrow, ca. 1 µm wide. The exine is faintly scabrate, tectate with an ektexine bridge frequently present over the pore; pseudocolpi are shorter than the colpi (7–9 µm) and represented by thinned mesocolpal regions with increased granulation of the exine (Fig. 19). The poles are circular, located at the midpoint of the colpus, 2.5–3 µm in diam. The grain size is 22–26 µm long (P) × 16–20 µm wide (E) at the equator.

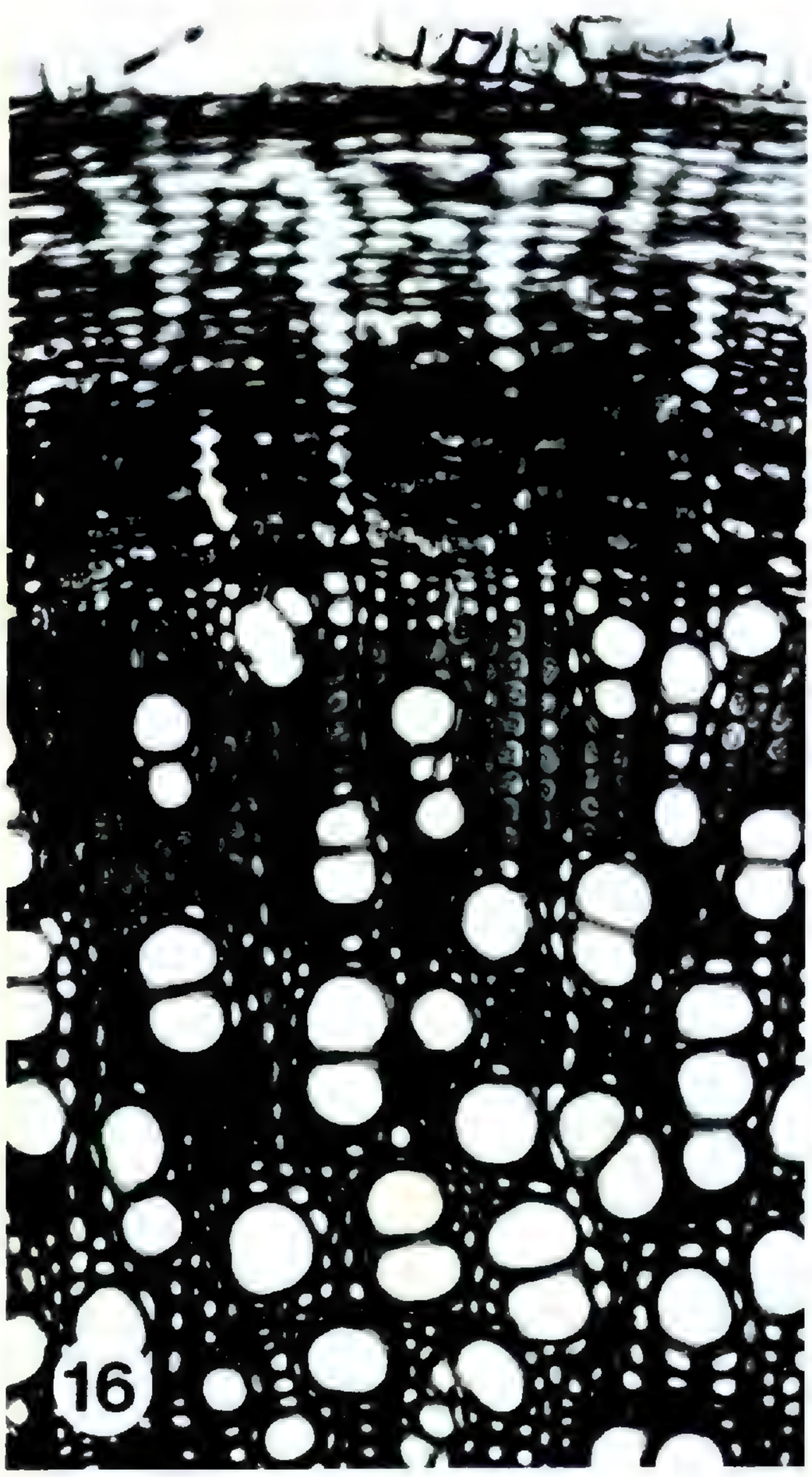
RELATIONSHIP TO *PEMPHIS ACIDULA*

The great difference between the two species currently assigned to *Pemphis* is apparent in comparative summaries of their reproductive and anatomical characters (Tables 1, 2). The most striking floral features of *P. madagascariensis* are the distinctive glandular trichomes and conspicuous ovary stipe, both of which are lacking in *P. acidula*. In addition, the combination of septifragal marginicidal capsule dehiscence, doubled condition of episepalous stamens and bilevel stamen insertion, strongly reflexed calyx lobes, restricted stigma development, limited basal production of nectariferous tissue, and the specialized elongated inner epidermal cells of the ovary wall clearly set *P. madagascariensis* apart from *P. acidula*. In contrast, *P. acidula* has circumscissile capsule dehiscence, single stamens inserted at one level, erect calyx lobes, bilobed stigma, nectariferous tissue lining the floral tube to the level of stamen insertion, and specialized tanniferous cells in the upper one-third of the ovary that harden in association with its circumscissile dehiscence mode. The morphology of the flower in *P. acidula* is related to its distylic condition (Lewis, 1975; Gill & Kyauka, 1977). The flowers of *P. madagascariensis* are homomorphic. The seeds are similar but much smaller in *P. madagascariensis* than in *P. acidula*.

The difference in vestiture between the two taxa is another indicator of their disparity. Both are well adapted to xerophytic habitats, but the trichome complements are entirely different. In *Pemphis madagascariensis* a mixture of sessile, globose, glandular hairs and unicellular, falcate, non-glandular hairs occurs (Figs. 12, 13). In *P. acidula* the dense seriaceous indument is composed entirely of long, straight, thick-walled, unicellular hairs ringed by a basal collar of the thickened epidermal cell wall (Figs. 10, 11).

Pollen differences between the two species are as great as between any two genera in the family. The pollen of *Pemphis madagascariensis* is tricolporate with three faint pseudocolpi, one to each mesocolpal area, and the exine is faintly scabrate (Figs. 18–20, 24). The pollen of *P. acidula* is twice as large and is consistently tetracolporate (ca. 1% tricolporate) with eight faint pseudocolpi, two to each mesocolpal area. The exine is characteristically psilate to faintly scabrate (Figs. 21–23).

From the summary of important anatomical attributes (Table 2), it is clear here again that *Pemphis madagascariensis* and *P. acidula* show many striking and significant differences. The anatomical characterization of *P. acidula*, particularly, stands out from all Lythraceae, including *P. madagascariensis*, by its conspicuous vasicentric xylem parenchyma, and by other anatomical features (Baas & Zweypfenning, 1979). Only a few of these can be interpreted as spe-



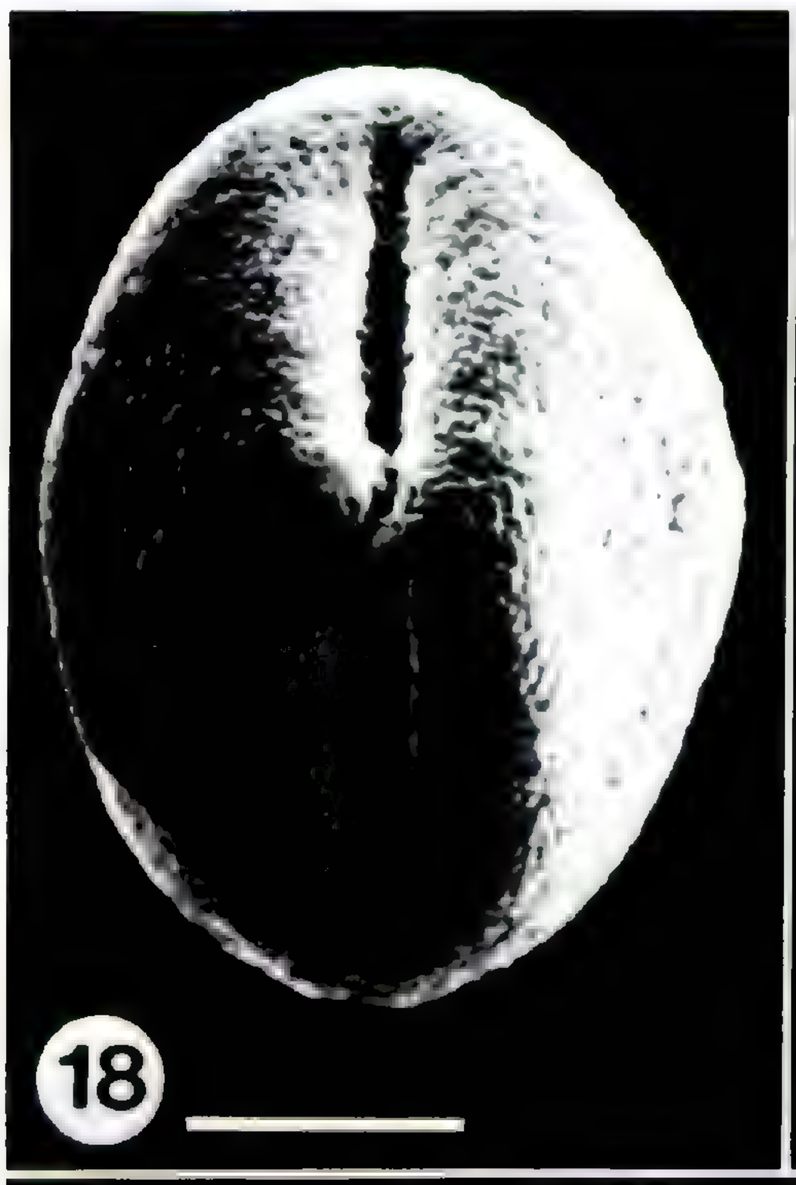
FIGURES 16, 17. Stem anatomical sections of *Koehneria madagascariensis*.—16. Transverse section of stem showing cork, cortex, phloem and secondary xylem, ×135.—17. Radial longitudinal section through the secondary xylem showing septate fibers (left) and narrow vessel elements (right), ×540.

cializations related to its xerophytic habit (thick isobilateral leaves with stomata on both sides; cf. Kienholz, 1926). Vegetative anatomy unambiguously supports separation of the two taxa.

Features shared by *Pemphis madagascariensis* and *P. acidula,* such as actinomorphic flowers and diplostemonous stamens with long episepalous filaments, are common to most genera of the Lythraceae. The generalized nature of these characters does not negate their inclusion in this comparison but does invalidate their usefulness as indicators of phylogenetic relationship. All evidence suggests there is no direct relationship between *P. madagascariensis* and *P. acidula.* Support for removal of the former from the genus *Pemphis* is well founded on all grounds investigated. The new generic name, *Koehneria,* is henceforth used in this discussion in place of *Pemphis madagascariensis.*

RELATIONSHIP TO *LAGERSTROEMIA*

The original disposition of *Koehneria* as a species of *Lagerstroemia* appears to have been made through ignorance of the definitive characters of *Lagerstroemia* or incomplete knowledge of the fruiting condition of *Koehneria. Lagerstroemia* uniquely has unilaterally winged seeds with a pyramidal seed body and revolute cotyledons. In addition, its inflorescences are multi-flowered racemes or panicles, the ovary is sessile, and the capsule is loculicidally dehiscent. In *Koehneria* the seeds lack wings and have straight cotyledons, the flowers are mostly solitary and axillary, the ovary is stipitate, and the capsule is septifragally dehiscent. Metcalfe and Chalk (1950) recorded glandular trichomes for *Lagerstroemia,* but this is apparently based on *L. madagascariensis.* Furtado and Srisuko (1969)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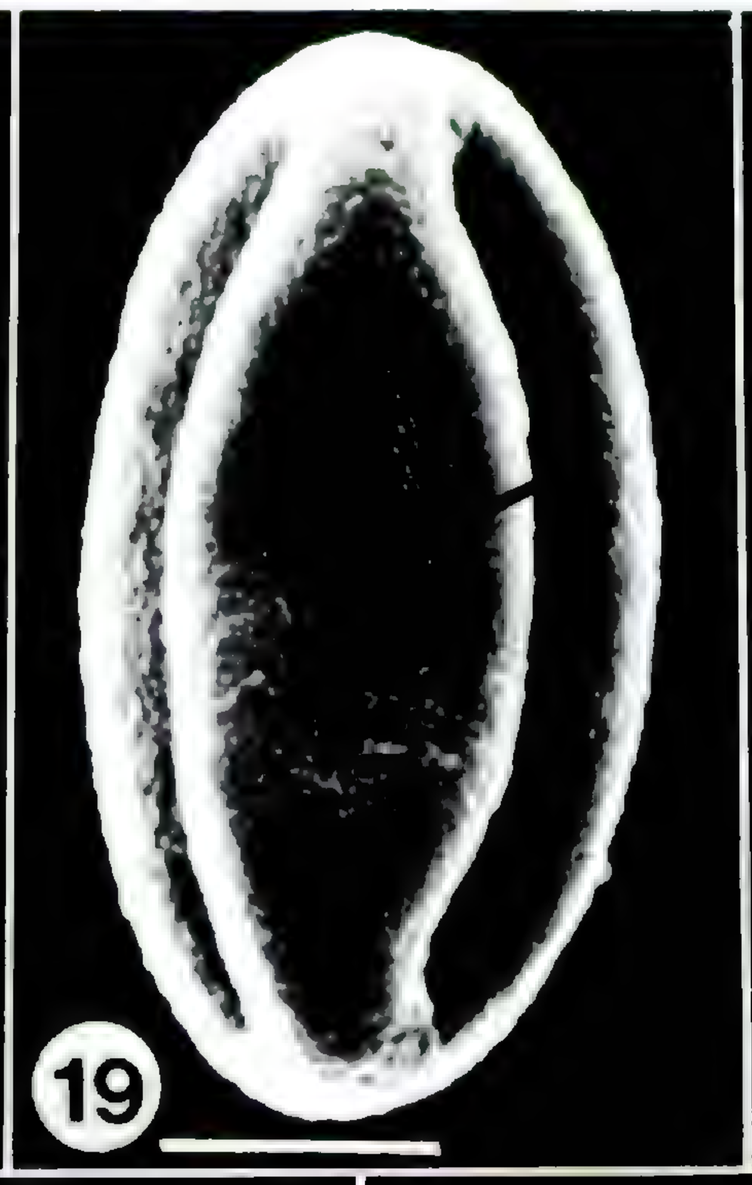
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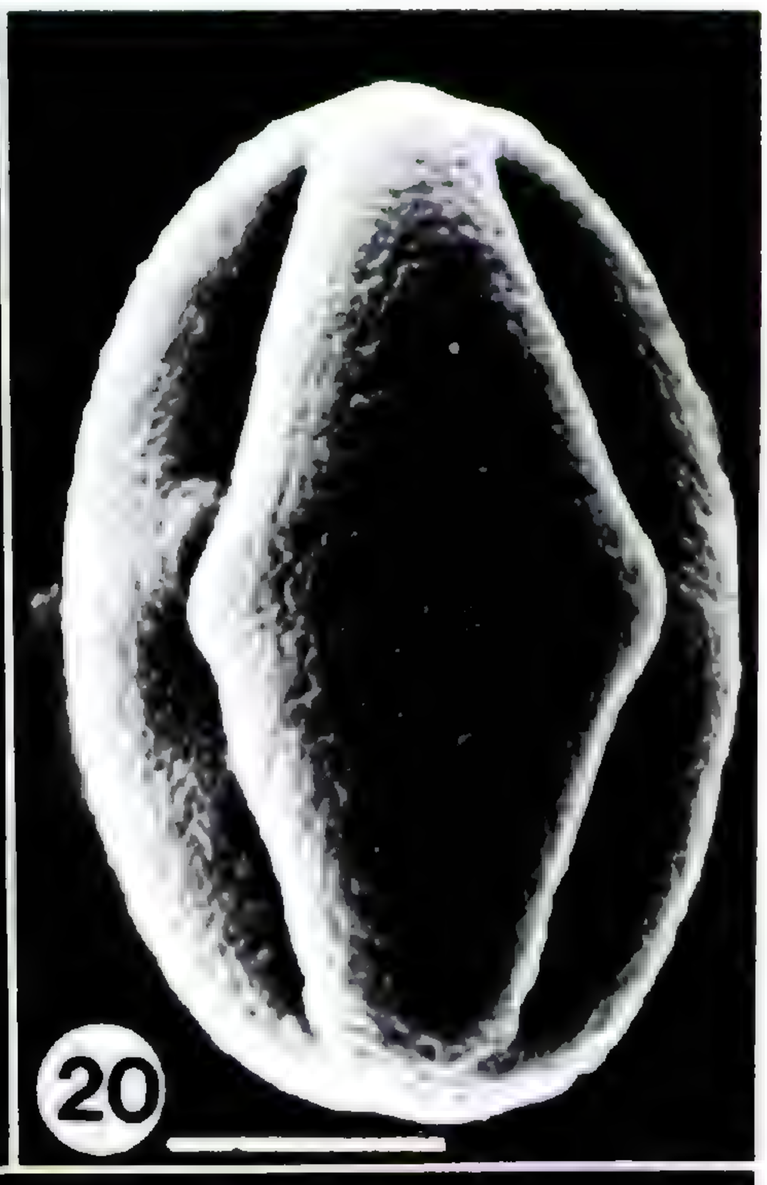
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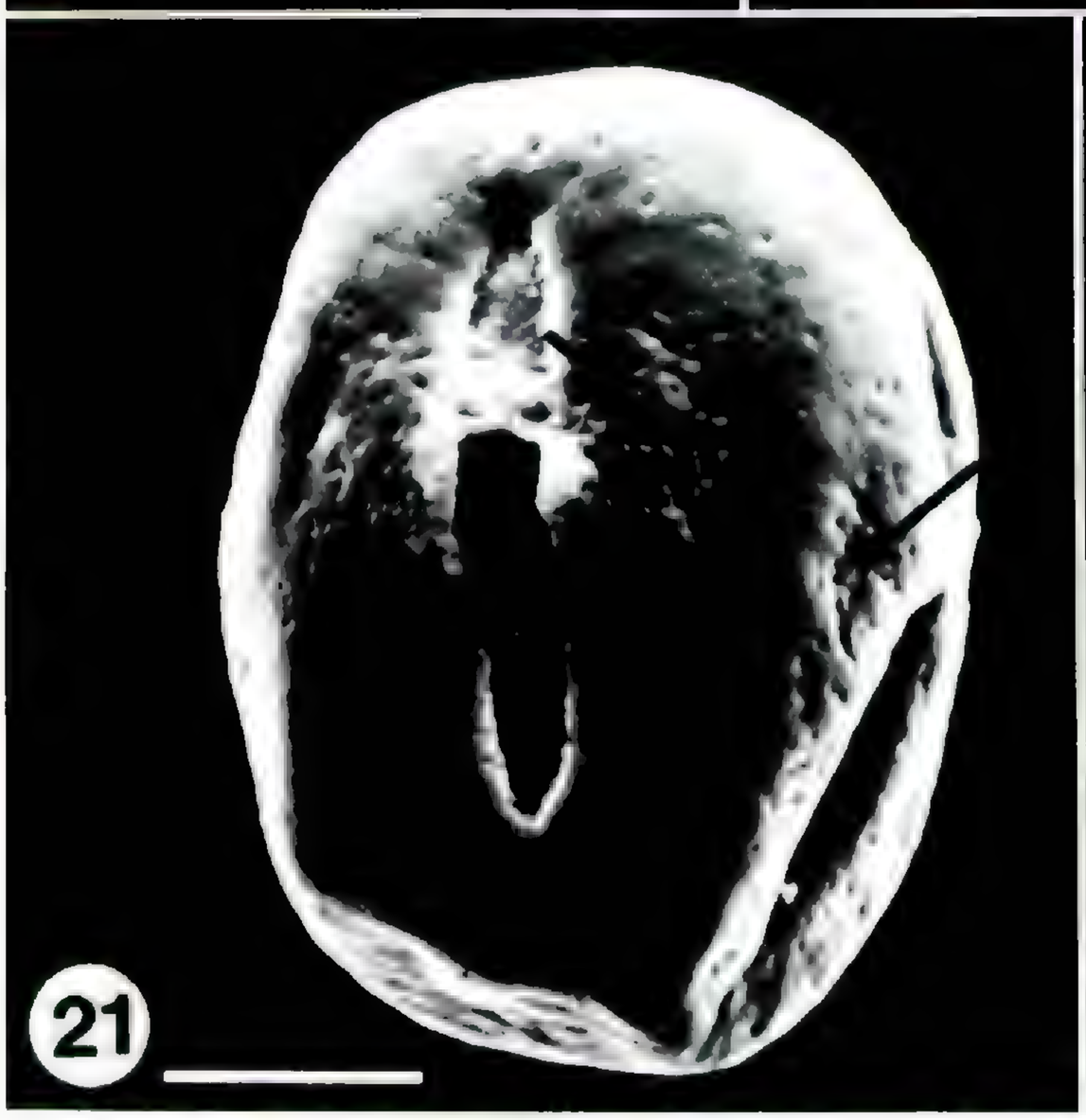
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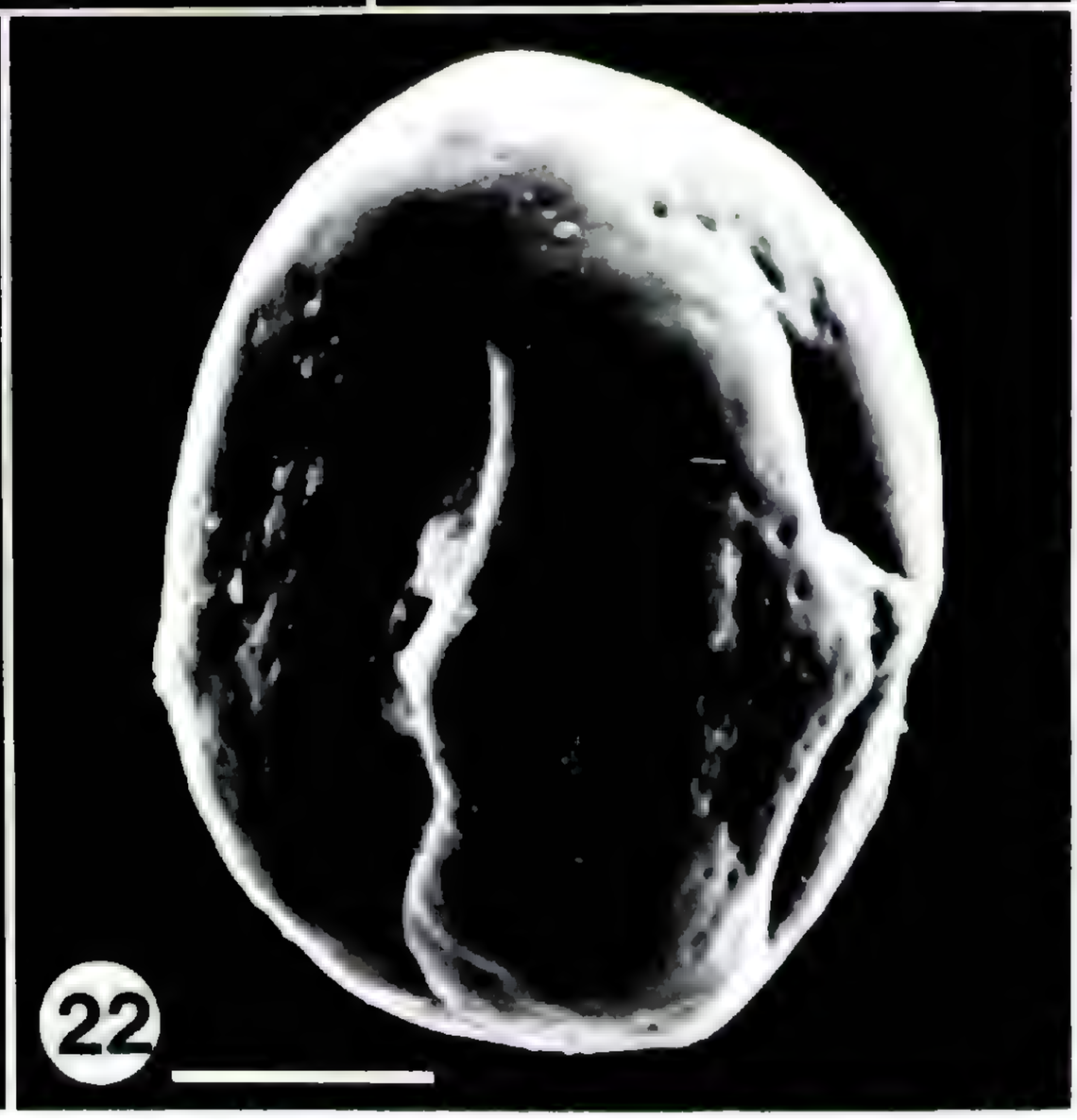
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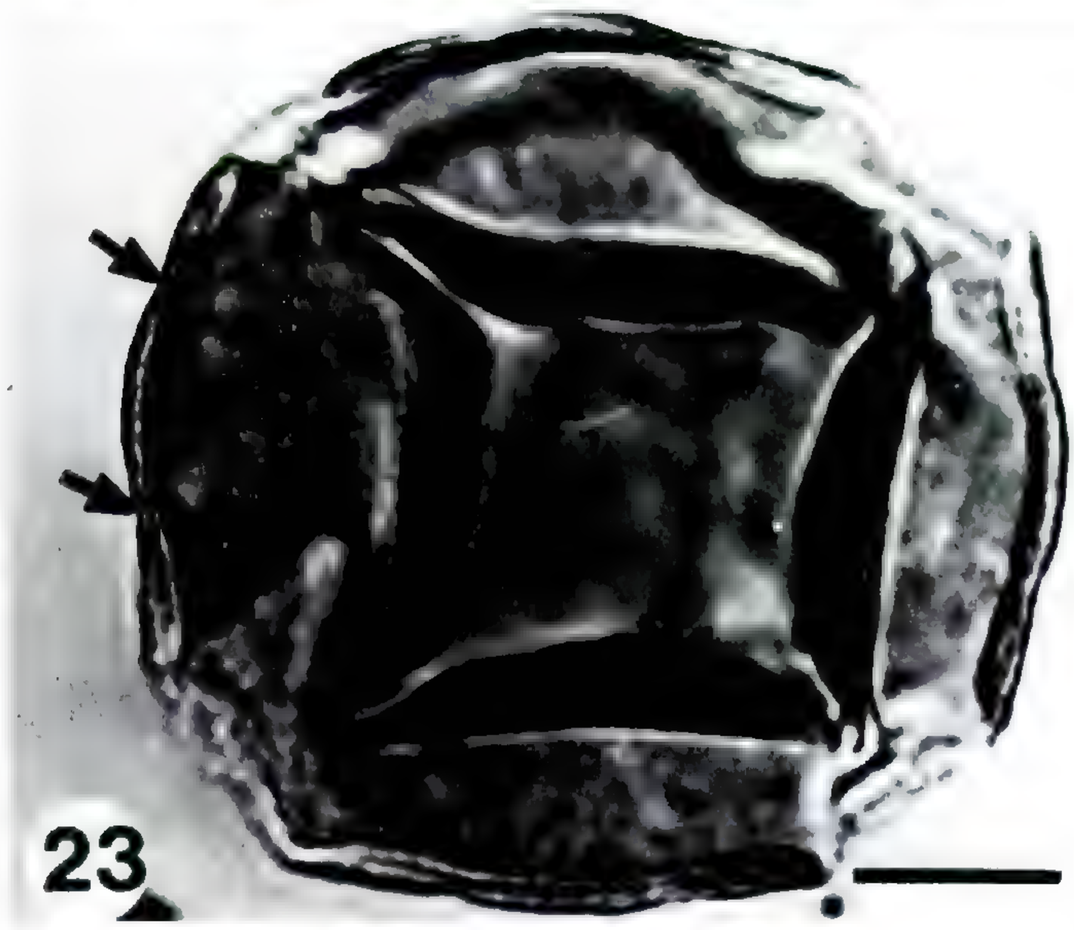
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loosely applied the terms "dotted" and "gland-dotted" to the leaves of a number of *Lagerstroemia* species, but glands were not found on herbarium specimens at Leiden of some of those species. Both Koehne (1903) and Furtado and Srisuko (1969) indicated that *L. ovalifolia* Teysm. & Binnend. has leaves that are black-punctulate beneath, and thus they might bear glands comparable to those of *Koehneria.* Examination of leaves of this species from four countries, however, revealed no glandular trichomes but instead numerous large subepidermal secretory cavities. These are especially abundant on the lower leaf surface and macroscopically appear as dark, not black, punctae after specimens are dried. Glandular trichomes of the *Koehneria* type probably are absent from all *Lagerstroemia.*

Similarities in wood anatomical characteristics of *Lagerstroemia* and *Koehneria* (Table 2) are plesiomorphic in nature, whereas the numerous wood anatomical features in which they differ are clearly apomorphic and indicate that sizable phylogenetic distance separates the two entities. Pollen features of each, likewise, indicate only their distant common ancestral origin; they suggest no close relationship between the taxa. *Lagerstroemia* is the only genus of Lythraceae with a center of speciation in southeastern Asia. No native species are found either in Africa or Madagascar. The species closest to Madagascar occur 4,000 miles to the northeast in Indonesia. From all evidence, there is no close phylogenetic affinity between the two genera and Koehne was unquestionably correct in removing *Koehneria* from *Lagerstroemia.*

Relationships to Other Lythraceae

Koehneria is unique in the Lythraceae in possessing the following suite of apomorphies: solitary, axillary, 6-merous flowers with strongly reflexed lobes; 18 stamens, of which 12 appear as pairs on the six sepals; a conspicuous elongate ovary stipe; elongate inner epidermal cells of the ovary; a septifragally dehiscent capsule; and globose, glandular trichomes on vegetative and floral parts. Among all other members of the family, the genus bears closest resemblance to the New World genera *Adenaria* and *Pehria,* and the Afro-Asian genus *Woodfordia,* by the appearance in all of the unusual globose glandular trichomes, an ovary stipe, and enlarged inner epidermal cells of the ovary wall (Table 3). These synapomorphies are unknown elsewhere in the Lythraceae and point to close common origin of the genera. Two other lythraceous genera, the zygomorphic New World *Pleurophora* and some species of the New World *Lafoensia,* possess a similar ovary stipe but lack other specialized characters that would ally *Koehneria* with this group. The stipe is regarded as having evolved independently in these taxa. In *Woodfordia* the ovary stipe is much less developed than in the other genera. In some specimens it appears to be absent; the nectariferous tissue then is fused directly to the base of the ovary. In other specimens, a very short stipe, free from the surrounding nectary, is discernible.

Some variation exists in the glandular trichomes as well. In *Woodfordia* and *Adenaria* a canalicular apical extension may develop on some glandular trichomes. This form was first observed in *Woodfordia* (Shome et al., 1981) and now is also noted in *Adenaria.* The necked form is restricted in *Woodfordia* to the outer surface of the floral tube and pedicel (Fig. 27); the stems and leaves bear the globose form (Figs. 25, 26). In *Adenaria* necked glandular trichomes, identical in appearance to those of *Woodfordia,* are seen sparsely mixed with globose forms on the ovary only on specimens from southeastern

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Figures 18–24. Pollen of *Koehneria madagascariensis* and *Pemphis acidula.*—18. Scanning electron micrograph of *K. madagascariensis,* equatorial view of a colpus with ektexine bridge.—19. Scanning electron micrograph of *K. madagascariensis,* equatorial view of slightly collapsed grain emphasizing location of pseudocolpus (indicated by arrow).—20. Scanning electron micrograph of *K. madagascariensis,* equatorial view of fully expanded grain, faint pseudocolpus flanked by colpi.—21. Scanning electron micrograph of *P. acidula,* equatorial view showing pore, colpus, and two faint pseudocolpi (indicated by arrows).—22. Scanning electron micrograph of *P. acidula,* equatorial view, the mesocolpal area at the center of the grain.—23. Light micrograph of *P. acidula,* polar view illustrating tetracolporate condition and faint pseudocolpi (indicated by arrows).—24. Light micrograph of *K. madagascariensis,* polar view, illustrating tricolporate condition and faint pseudocolpi (indicated by arrow). Scale equals 5 μm in Figures 18–20; 10 μm in Figures 21 and 22; 10 μm in Figures 23 and 24. Figures 18–20 from *D'Arcy & Rakotozafy 15317* (MO); Figures 21 and 22 from *Kibiwa 1204* (MO); Figure 23 from *von Mueller 3* (K); Figure 24 from *Lam & Meeuse 5430* (K).

TABLE 1. Comparison of *Koehneria* with *Pemphis, Lagerstroemia,* and putative allies. Data based on observations of the authors and on Koehne (1903).

Characters	*Koehneria*	*Pemphis*	*Adenaria*	*Pehria*	*Woodfordia*[a]	*Lagerstroemia*
Number of species	1	1	1	1	2	53
Geographic distribution	Madagascar	E. Africa & Madagascar to Pacific	SE Mexico to N. Argentina	Honduras to Colombia	E. & W. Africa (1 sp.) & Madagascar & E. Asia (1 sp.)	E. & W. Asia, W. Pacific
Inflorescence	solitary, axillary	solitary, axillary	compact, much-branched cyme, dense, umbelliform	compact, much-branched cyme, few-flowered, loose	compact, much-branched cyme, few-flowered, loose	racemose or paniculate
Leaves	thick, ± coriaceous	thick, fleshy	herbaceous, dry	herbaceous, dry	thick, ± coriaceous	primarily herbaceous
Floral morphology						
Floral forms	monomorphic	dimorphic	trimorphic	monomorphic	monomorphic	monomorphic
Symmetry	actinomorphic	actinomorphic	actinomorphic	actinomorphic, weakly zygomorphic	weakly zygomorphic	actinomorphic
Merosity	6-merous	6-merous	4 (or 5)-merous	4 (or 5)-merous	(4–)6-merous	(4–)6(–8)-merous
Shape	campanulate	campanulate	campanulate	cyathiform	cyathiform to tubular	campanulate
Length	4.5–8.5 mm	4.0–7 mm	2.5–4.5 mm	5.0–9.0 mm	9.0–15(–20) mm	5–17 mm
Lobe position	strongly reflexed	erect	erect	weakly reflexed or erect	erect	erect to reflexed
Epicalyx length	0.0–2 mm	ca. 0.5 mm	0.0 mm	0.2–0.5 mm	0.2–0.3 mm	0.0–2 (?) mm
Petal number	6	6	4 (5)	4 (5)	(4) 6	6+
Petal shape	broadly obovate	elliptic	obovate–oblanceolate	narrowly lanceolate	narrowly lanceolate	ovate–obovate
Petal size	5.5–10 mm × 4.0–7 mm	7.5–8.0 mm × 5.5–6.0 mm	4.0–4.2 mm × 1.0–1.2 mm	4.2–4.5 mm × 1.3–1.6 mm	1.0–3.0 mm × 0.2–0.5 mm	5–25 mm × 3–20 mm
Petal color	rose-purple	white	white (or pale rose)	red	red	rose-purple, white
Stamen number	(16–)18(–20)	12	8 (10)	8 (10)	(8) 12	15–200
Stamen position	episepalous doubled, epipetalous single	episepalous & epipetalous single	episepalous & epipetalous single	episepalous & epipetalous single	episepalous & epipetalous single	episepalous single or numerous, epipetalous numerous

TABLE 1. Continued.

Characters	*Koehneria*	*Pemphis*	*Adenaria*	*Pehria*	*Woodfordia*[a]	*Lagerstroemia*
Stamen chorisis	present in episepalous stamens	absent	absent	absent	absent	present in episepalous & epipetalous, or epipetalous stamens only
Stamen lengths	episepalous longer	episepalous longer	all ± equal	all ± equal	episepalous longer	episepalous longer or all equal
Ovary shape	globose	turbinate	turbinate	globose	±fusiform	globose–oblong
Locule number	2 or 3	3	2	2	2	3–6
Ovary stipe	present	absent	present	present	present, very short, to absent	absent
Style length	7–15 mm	1–5 mm	1–4 mm	7–8 mm	13–14 mm	variable, exceeding stamens
Stigma shape	punctiform	capitate	distinctly bilobed	punctiform	punctiform–barely capitate	punctiform
Trichomes						
Non-glandular on leaf	unicellular, falcate	unicellular, elongate with thick base, stiff	unicellular & multicellular, weak	unicellular & multicellular, weak	unicellular, falcate	various
Glandular						
Shape	globose	absent	globose, globose with neck	globose	globose, globose with neck	absent
Location on floral parts	outer floral tube & upper half of ovary	absent	outer floral tube, upper half of ovary, petals	outer floral tube, petals	outer floral tube	absent
Nectaries	present, base of floral tube	present, from base to stamens	present, from base halfway to stamens	present, from base to stamens	present, base of floral tube	absent
Ovary wall thickness	4–5 cells	7–20 cells	8–9 cells	6–7 cells	6–7 cells	?
Ovary wall specialization	inner epidermal cells enlarged	cells of upper ⅓ of ovary tanniferous & solidified	inner epidermal cells enlarged	inner epidermal cells enlarged	inner epidermal cells enlarged	?

TABLE 1. Continued.

Characters	*Koehneria*	*Pemphis*	*Adenaria*	*Pehria*	*Woodfordia*[a]	*Lagerstroemia*
Capsule dehiscence	septifragal–marginicidal	circumscissile	indehiscent	loculicidal, splitting adaxially	indehiscent or splitting variously, incl. loculicidal	loculicidal
Seed size	1.2–1.3 mm × 0.9–1.0 mm	3.0–3.2 mm × 1.5–1.9 mm	0.9–1.1 mm × 0.5–0.6 mm	0.7–0.9 mm × 0.3–0.4 mm	0.7–0.8 mm × 0.4–0.5 mm	7–12 mm × 3–5 mm
Seed wing	absent	absent	absent	absent	absent	present
Seed hairs	absent	absent	absent	absent	present	absent
Cotyledon position	plane	plane	plane	plane	plane	revolute
Pollen morphology						
Colpi number	3	4	3	3	3	3
Pseudocolpi	3 faint, 1/mesocolpus	8, 2/mesocolpus	0	0	0	0 or 6 faint, 2/mesocolpus
Exine sculpture	faintly scabrate	psilate–faintly scabrate	scabrate	scabrate	scabrate	verrucate
Size (P × E)	19–26 μm P × 14–20 μm E	40–55 μm P × 35–54 μm E	18–22 μm P × 16–20 μm E	22–28 μm P × 16–18 μm E	16–22 μm P × 12–16 μm E	35–55 μm P × 25–46 μm E
Chromosome nos.	unknown	$2n = 32$	$2n = 32$	$2n = 32$	$2n = 16$	Various, $2n = 16$–50

[a] Data based primarily on *Woodfordia fruticosa* in this ditypic genus.

TABLE 2. Anatomical character summary of *Koehneria* and putative allies.

	Koehneria	*Pemphis*	*Adenaria*	*Pehria*	*Woodfordia*	*Lagerstroemia*[a]
Leaf Anatomy						
Unicellular hairs broad-based	+	−	+	±	+	±, − ?
Globose glands present	+	−	+	+	+	−, ?[b]
Stomata on both leaf surfaces	−	+	+	−, +	−	−
Epidermal mucilage cells	++	++	++	−, +	−, +	+
Lamina isobilateral	−	+	−	−	−	+, −
Major veins vertically transcurrent	+	−	+	+	+	+
Wood Anatomy						
Fibers septate	+	−	+	+	±	+
Parenchyma scanty or absent	+	−	+	+	+	−[c]
Rays mainly of erect cells	+	−	±	+	+	−

[a] Leaf anatomical data on *Lagerstroemia* are scanty considering the large number of species.

[b] Metcalfe and Chalk (1950) recorded glands for *Lagerstroemia,* and Furtado and Srisuko (1969) described a number of *Lagerstroemia* species with (gland-) dotted leaves; these records could not be confirmed (see also text).

[c] One group of *Lagerstroemia* species has scanty parenchyma but is characterized by conspicuous fiber dimorphism, a feature absent from *Koehneria.* The other species of *Lagerstroemia* have abundant parenchyma.

++ = character very pronounced or abundant; + = character present; ± = character weakly pronounced or infrequent.

Mexico [*R. Torres 1369, Breedlove 25581, 38133,* (KE-Graham)]. None have been seen on collections from Central or South America. Trichomes vary in the length of the neck produced. In *Woodfordia* they can be seen in all stages of development from the common globose form to short- or long-necked forms. The thick orange content, possibly resin, extends part way into the neck but is not extruded at the apex as in typical glandular trichomes. There is no evidence on which to determine whether the globose or necked form is the derived state. However, if the globose gland is derived from a typical multicellular gland through loss of the apical extension, the loss is nearly complete, being retained on limited parts of the flower only. Multicellular glandular hairs are uncommon in the family (common only in *Cuphea* and *Pleurophora*); have a broad multicellular base rather than a narrow, nearly stalked one; and produce a clear, sticky resin unlike the thick orange contents of the globose glands. This suggests globose glands are not homologous to other multicellular glandular trichomes in the Lythraceae but may be a new trichome type developed in the ancestor of this group of genera.

Anatomical attributes of *Koehneria* are closely comparable to those of *Pehria, Woodfordia,* and *Adenaria* (Table 2). *Pehria* differs by possessing specialized chambered crystalliferous fibers (Baas & Zweypfenning, 1979). This difference, however, does not preclude close phylogenetic affinity and, on the whole, anatomy supports the association of the genera circumscribed by the trichome and ovary characteristics.

The pollen of *Koehneria* differs from that of *Adenaria, Pehria,* and *Woodfordia* by the presence of faint pseudocolpi. *Koehneria* pollen, however, does not display any specialized features that point to a specific generic relationship. Several genera or portions of genera show the same general shape, triporate condition, and exine sculpturing seen in *Koehneria.* These include *Adenaria, Pehria,* and *Woodfordia,* but also the distantly related *Physocalymma, Heimia,* and some species of *Lagerstroemia.* The pollen data do not rule against a close alliance with *Adenaria, Pehria,* and *Woodfordia* but provide no direct evidence for any more specific relationship.

Although they share a number of specialized morphological and anatomical features, genera of this alliance differ to a substantial degree from each other (Table 3). *Adenaria* is a monotypic, small-shrub genus of New World seasonally evergreen and semievergreen forest zones. Its leaves are herbaceous with glands and uni- and multicellular weak hairs, which are most abundant along the veins on the abaxial side of the leaf (Fig. 29). The four-merous flowers with erect calyx lobes appear in dense umbelliform axillary clusters and are weakly tristylic. There are three

Table 3. Comparison of selected morphological features of **Koehneria, Adenaria, Pehria,** and **Woodfordia.** Derived characteristics shared between two or more genera boxed; characteristics unique to a genus bold-boxed.

Character	Koehneria	Adenaria	Pehria	Woodfordia
Inflorescence	solitary, axillary flower	compact, much branched cyme, umbelliform clusters	compact, much branched cyme, open clusters	compact, much branched cyme, open clusters
Leaf texture	±coriaceous	herbaceous	herbaceous	±coriaceous
Floral forms	monomorphic	trimorphic	monomorphic	monomorphic
Floral symmetry	actinomorphic	actinomorphic	actino- to weakly zygomorphic	weakly zygomorphic
Merosity	6-merous [a]	4-merous	4-merous	6-merous
Shape	campanulate	campanulate	cyathiform	cyathiform to tubular
Calyx lobes	strongly reflexed	erect	weakly reflexed to erect	erect
Petal shape	broadly obovate	obovate - oblanceolate	narrowly lanceolate	narrowly lanceolate - linear
Petal color	rose-purple	white to rose	red	red
Stamen number	18	8	8	12
Stamen lengths	2 lengths	1 length	1 length	2 lengths
Paired episepalous stamens	present	absent	absent	absent
Stigma	punctiform	bilobed strongly	punctiform	punctiform
Ovary stipe	present, long	present, long	present, long	present, very short to absent
Globose glands	present	present	present	present
Nectary	basal, well-separated from stamens	basal one-half distance to stamens	basal to stamens	basal, well-separated from stamens
Ovary inner epidermal cells	enlarged	enlarged	enlarged	enlarged
Capsule dehiscence	septifragal-marginicidal	indehiscent	loculicidal	indehiscent or splitting variously
Seed hairs	absent	absent	absent	present, spiral
Pollen pseudocolpi	3, faint	0	0	0

a. Polarity of floral merosity at the family level in Lythraceae is not clear. Both the 4- and 6-merous condition may have been derived from an ancestral 5-merous one. Flowers of ca. one-half the genera vary from 3-5-merous, but are basically 4-merous, while the remaining genera vary from 5- to 6-merous, but are most commonly 6-merous. Another view regards 6-mery as primitive in the family (Tobe, unpubl. data).

stamen lengths, but within a single flower there is only one stamen whorl and the filaments are more or less equal in length (Nevling, 1958). The breeding system of the genus has not been fully explored but limited pollen viability data suggest the genus might be evolving from heterostyly to dioecy in a way similar to that observed in certain heterostylous Rubiaceae (Bawa, 1980). In two collections of short-styled flowers, 44% viable grains were produced (based on counts of 500

grains stained in cotton blue-lactol phenol). In one intermediate-styled collection pollen was 60% viable. In contrast, flowers from four long-styled collections formed no pollen, the microsporangia in each instance containing amorphous, dark-stained contents (Graham, unpubl. data). Other characteristics of *Adenaria* not found in *Koehneria* are the unusual (for Lythraceae) deeply bilobed stigma, more extensively developed nectariferous tissue, and indurate, indehiscent capsule.

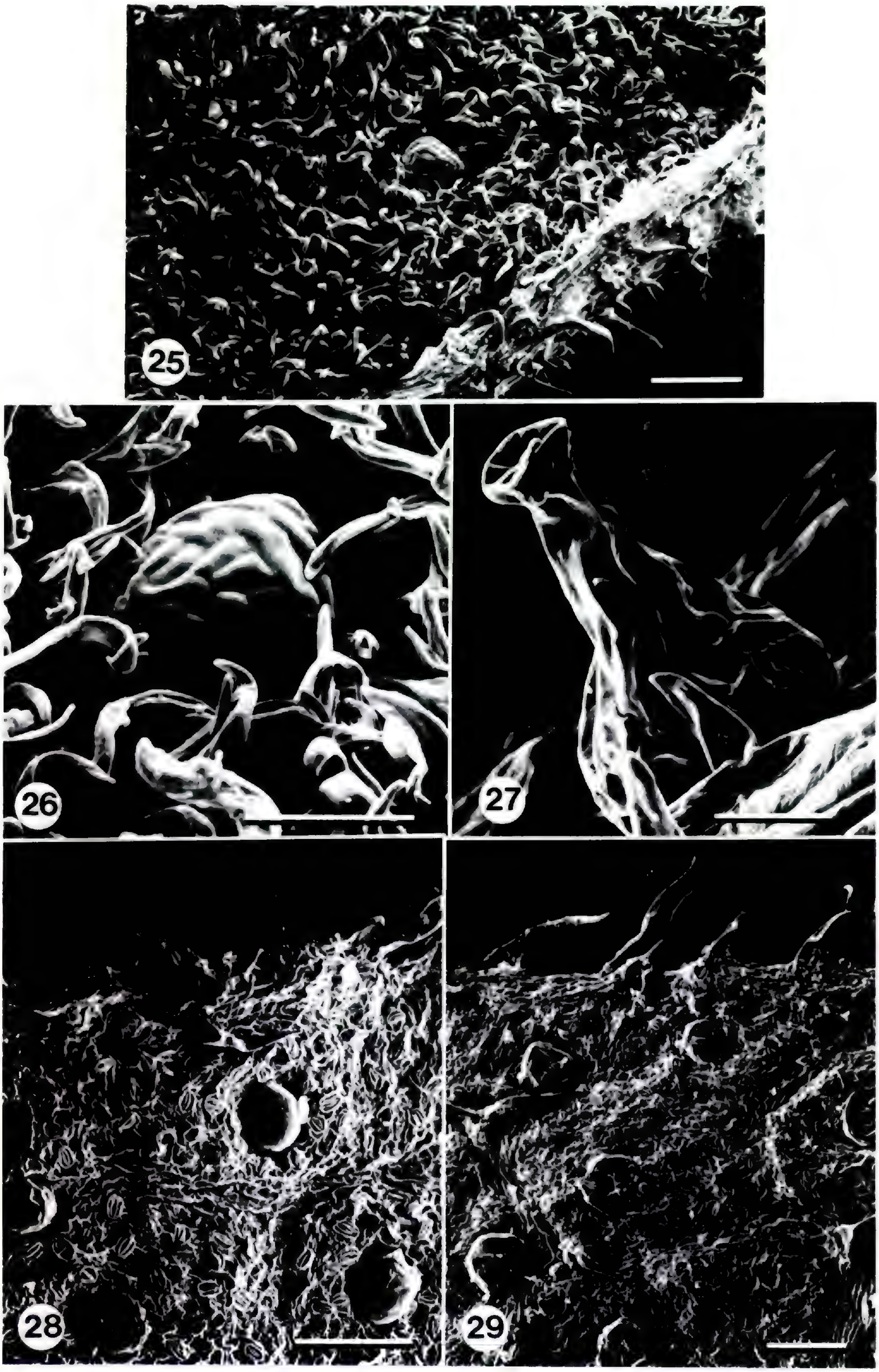
Pehria is similar to *Adenaria* in habit and distribution. It is also a monotypic shrub genus of Central and northern South America found at elevations from 90 to 1,300 m in a variety of habitats ranging from dry deciduous woods to pine-oak and tropical cloud forests. Its leaves, like those of *Adenaria,* are herbaceous, without tomentose indument, and, in addition to the globose glands, bear mostly multicellular, uniseriate, weak trichomes mixed with sparser short unicellular ones (Fig. 28). The flowers are 4-merous, as in *Adenaria,* but are monomorphic with a more elongate floral tube, deep red petals, a punctiform stigma, extensive nectary development extending from the base of the ovary to the stamen insertion, and thin-walled, loculicidally dehiscent capsules. *Adenaria* and *Pehria* are more similar morphologically than either is to *Koehneria*; anatomically *Koehneria* and *Adenaria* are most similar.

The genus *Woodfordia* comprises two species of shrubs of semixeric habitats. *Woodfordia uniflora* is found in Nigeria, Cameroon, eastern Sudan, Ethiopia, and Uganda (Keay, 1954). *Woodfordia fruticosa* grows with *Koehneria* in Madagascar (possibly as an early introduction because of its alleged aphrodisiacal properties?) and further ranges from Pakistan through northern India and southern China to Sumatra, Java, and Timor. In total leaf vestiture *W. fruticosa* and *Koehneria* are virtually identical in having slightly sunken glandular trichomes interspersed in a dense cover of unicellular falcate hairs (cf. Figs. 12, 13, 25, 26). The leaf texture is also similar, although slightly more coriaceous in *Koehneria.* Similarities in leaf vestiture may be attributed to a close phylogenetic relationship, although it is also possible this is the result of evolutionary convergence as a response to the similar environmental stress imposed by the seasonally dry habitats in which these two genera occur.

In most other derived characteristics, beyond the previously mentioned shared trichome and ovary characters, *Koehneria* and *Woodfordia* are dissimilar. The flowers of *Woodfordia* are six-merous as in *Koehneria* but have elongate tubes that appear weakly zygomorphic due to the arrangement of stamens and style on the lower side of the flower and to the frequent splitting of the persistent floral tube and enclosed capsule along only the adaxial side of the flower at maturation. The same zygomorphic tendencies are also seen in *Pehria.* Its floral tube and petals are bright red and the ovary stipe is scarcely developed to absent, rather than conspicuous. A further apomorphy of *Woodfordia,* not present in the other genera of this group, is the spiral, inverted epidermal hairs of the seed coat. These unusual hairs occur in only three other genera of the family, in the zygomorphic genera *Cuphea* and *Pleurophora,* and in the actinomorphic *Lafoensia.* Most likely, they have been independently derived in *Lafoensia.* They are absent from the seed coat of *Koehneria, Adenaria,* and *Pehria.*

In summary, *Koehneria*'s nearest relatives are the genera *Adenaria, Pehria,* and *Woodfordia,* an interpretation based on a three-character synapomorphy unique to the group. Beyond sharing this character set, the genera have differentiated extensively and more specific relationships cannot be determined from present information. *Koehneria,* among the four, displays the most derived features (Table 3), but differentiation has occurred in different directions and at different rates for individual characters in each of the genera, making comparisons for purposes of establishing phylogeny difficult. For example, in *Koehneria* the inflorescence has been reduced to a solitary axillary flower, while at the same time the primitive campanulate flower shape and basal nectary have been retained. In *Woodfordia* a less advanced inflorescence type, i.e., numerous flowers in a basically cymose inflorescence, is combined with a more advanced elongate floral tube, in which the nectary has remained basal.

The present distribution of *Koehneria* and allied genera in two hemispheres apparently reflects an early and extensive dispersal from a common African center of origin. The earliest incontrovertible fossil records of the Lythraceae are from the lower Eocene London Clay flora and the Eocene Deccan Intertrappean beds of India and suggest an Old World, warm-temperate origin for the family (Graham & Graham, 1971). The diversity of taxa present in the Eocene indicates a history for the family extending at least back into the Paleocene. The fossil record in combination with distribution patterns of ex-



FIGURES 25–29. Scanning electron micrographs of trichomes of *Woodfordia fruticosa* [*USDA-Miami PI 19882* (KE-Graham)], *Pehria compacta* [*Ortiz 878* (KE-Graham)], and *Adenaria floribunda* [*Torres 1369* (KE-

tant lythraceous genera suggests east Africa as a plausible place of origin for the family. The distribution of the *Koehneria* alliance is consistent with this model. Migrations during the early Tertiary, to place *Adenaria* and *Pehria* or their ancestors in the American flora, would have been possible geologically and climatically, either westward to South America or via a north Atlantic land route (Raven & Axelrod, 1974; Smith et al., 1981). A history of overland dispersal of plant forms related to *Koehneria* finds some support from fossil evidence. Fossil seeds from the Miocene of Denmark have been related to modern *Koehneria* seeds (Friis, 1985). Identical seeds are recorded from the older Oligocene floras of England (Chandler, 1957) and the northeastern United States (Tiffney, 1981; flora presumed to be Oligocene) with affinities tentatively attributed to Lythraceae by the authors. A separate, later migration from Africa is necessary to explain the present distribution of *Woodfordia fruticosa* in Pakistan, northern India, southern China and islands southward. *Koehneria* may have evolved from ancestral, less xerophytic, forms in Africa and spread to Madagascar where it survives today, or it may have evolved in situ. Understanding of differentiation in this alliance and in the family generally would be greatly enhanced by discovery of fossil remains from the critical Paleocene epoch in Africa. In the absence of a substantiating fossil history, the present morphological and distributional patterns of *Koehneria* and relatives are regarded as the result of heterobathymic divergence and extensive dispersal coupled with widespread extinctions. These processes have obscured or erased evidence of the intervening history of the genera to the extent that determination of phylogenetic affinities of *Koehneria* may be made to the level of the four-genera alliance, but not to a specific modern genus.

Systematic Treatment

In view of the significant differences in morphological, anatomical, and palynological features, *Pemphis madagascariensis* is here assigned to the monotypic new genus *Koehneria*. The generic name honors B. A. Emil Koehne (12 Feb 1848–12 Oct 1918), Berlin, whose finely detailed and self-illustrated monograph of the Lythraceae remains today the single complete study of the family.

Koehneria S. A. Graham, H. Tobe & P. Baas, gen. nov. TYPE: *Koehneria madagascariensis* (Baker) S. A. Graham et al. ≡ *Lagerstroemia madagascariensis* Baker. ≡ *Pemphis madagascariensis* (Baker) Koehne.

Fam. Lythraceae. Frutex, alt. 0.5–2(–4) m, undique cinereo-tomentellus. Folia petiolis subnullis, oblonga, 15–70 mm longa, 5–20 mm lata, utraque pagina nigro-punctulata, necnon subtus tomentello-albicantia. Flores solitarii, nigro-punctulati, axillares, 6-meri, campanulati, lobis reflexis; petala 6, rosea; stamina 18, episepala gemina, epipetala singula altius inserta; ovarium globosum, breviter stipitatum, apice nigro-punctulatum; stylus longissime exsertus. Capsula 2–3 locularis, septifraga marginicidalis; semina numerosa, cuneato-compressa. Ab *Pemphis* s. str. differt pilis glanduliferis, staminibus 18, ovario stipitato.

Shrubs with ash-gray bark and short, terete branches bearing white indument; nodes slightly buttressed; buds ovoid to triangular, compressed. Leaves opposite, subcoriaceous, sessile or nearly so, oblanceolate to linear-oblong, both sides with black punctulate glandular trichomes, these denser on the abaxial side and interspersed in a tomentum of white, falcate, non-glandular hairs. Flowers solitary, or rarely 2, axillary, pedicellate, campanulate, glandular punctulate and pubescent, 6-merous, homomorphic; lobes strongly reflexed at anthesis, alternating with 6 short appendages (epicalyx). Petals 6, bright rose-purple, longer than the floral tube. Stamens (16–)18(–20), the episepalous ones paired, the epipetalous ones single and inserted higher in the tube. Pollen prolate-spheroidal, tricolporate with circular pore and 3 faint pseudocolpi, the exine faintly scabrate. Ovary globose, distinctly stipitate, 2–3-locular, glandular-punctate and lightly pubescent at the apex; style long exserted; stigma punctiform. Capsule dehiscence septifragal marginicidal; seeds deltoid- to cuneate-compressed; cotyledons flat.

A monotypic genus with the following species:

←

Graham)].—25. Tomentose lower leaf surface of *W. fruticosa*.—26. Multicellular, globose, glandular trichome surrounded by unicellular, non-glandular trichomes on lower leaf surface of *W. fruticosa*.—27. Multicellular, glandular trichome with neck on pedicel of *W. fruticosa*.—28. Lower leaf surface of *P. compacta* with globose glandular trichomes and stomata prominent.—29. Lower leaf surface of *A. floribunda* with globose glandular trichomes and elongate non-glandular trichomes prominent. Scale equals 100 μm in Figures 25, 28, and 29; 50 μm in Figure 26; 25 μm in Figure 27.

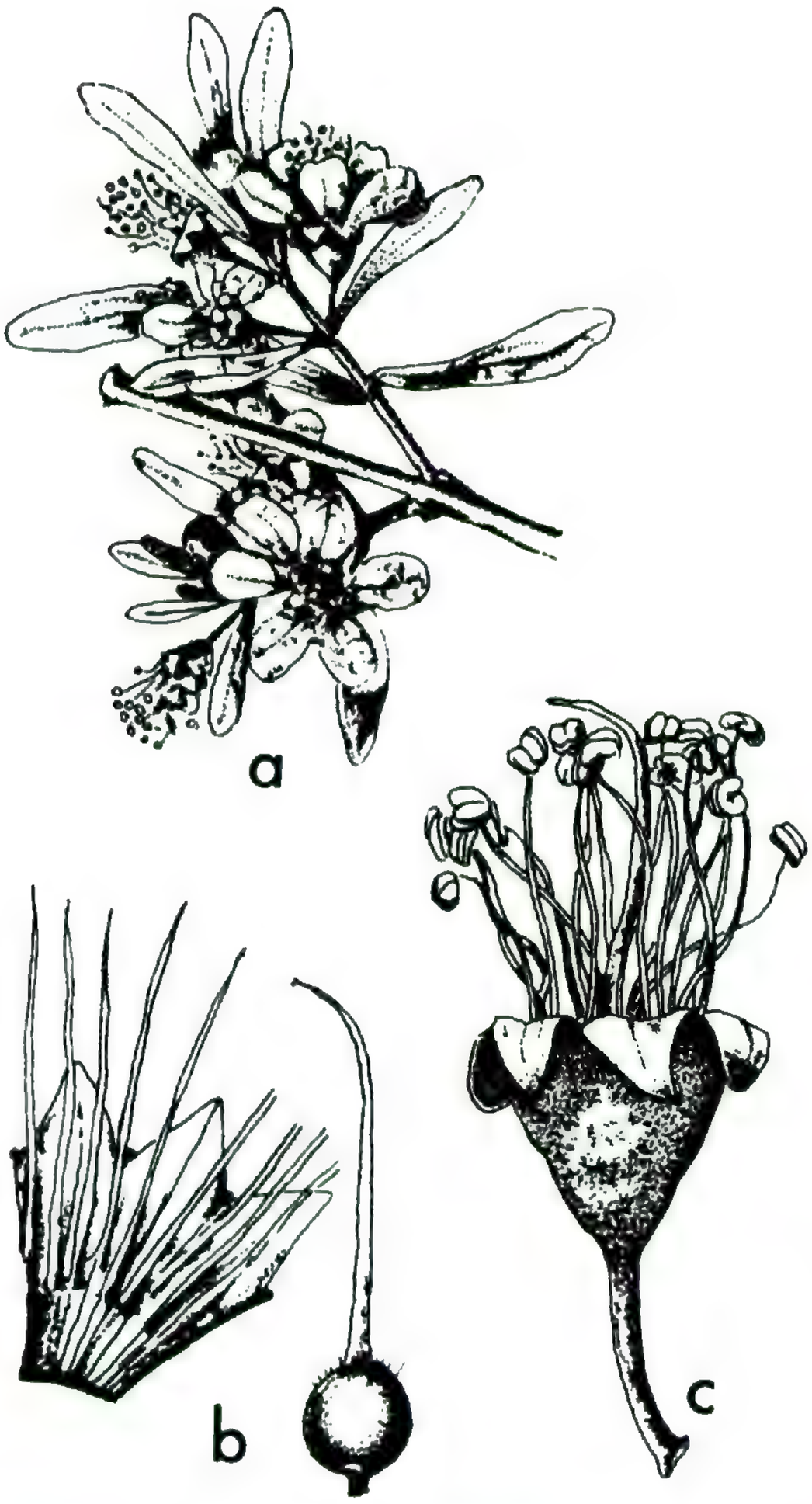


FIGURE 30. *Koehneria madagascariensis*. —a. Flowering branch, ×1.—b. Stamen insertion on opened partial floral tube and gynoecium, ×3.—c. Flower with reflexed lobes, ×3. From Koehne, 1903.

Koehneria madagascariensis (Baker) S. A. Graham, H. Tobe & P. Baas, comb. nov. (Fig. 30). *Lagerstroemia madagascariensis* Baker, J. Linn. Soc. (Bot.) 18: 270. 1881; J. Bot. (n. s.) 11: 112. 1882. *Pemphis madagascariensis* (Baker) Koehne, in Engler, A., ed., Das Pflanzenreich. IV. 216. Heft 17. p. 187. 1903. TYPE: Madagascar: "Ibara" (Bara) country, communicated May 1880, *Langley Kitching s.n.* (holotype, K!).

Pemphis punctata Drake del Castillo, Bull. Soc. Linn. Paris 2: 1222. 1896. LECTOTYPE here designated: Horombe, 18 Jun 1890, *Catat 4356* (P!). Two syntypes are cited in the protologue, *Catat 4356* and *4358*; both specimens present at P. The new species name is written on the label of *Catat 4356* in the hand of Drake, while the other specimen bears the name in the hand of a French botanist, P. Danguy (pers. comm., A. Lourteig, 1984). Since both syntypes are otherwise equally representative of the species, the specimen annotated by the author of the species is selected as lectotype.

Shrubs 0.5–2(–4) m tall, trunk diam. to 4 cm, with smooth ash-gray to gray-brown bark excorticating in very narrow to thread-like whitish strands, the inner bark red-brown; stems much branched, the branches terete, short, 4–10(–20) cm long, covered in fine, white or red-brown indument; nodes opposite, buttressed by the raised bases of the leaf scars, especially on the youngest branchlets; internodes telescoped toward the branch extremities with the season's leaves then tending to cluster at the ends of the branches; leaf scars semi-circular, projecting outward and tapering downward from the stem, bearing a row of red-purple, erect, thick, stipular processes adaxially between the scar and the stem, the processes falling away with age; buds ovoid to triangular in outline, compressed parallel to the stem surface. *Leaves* deciduous, opposite, entire, thick, rigid, subcoriaceous, sessile or nearly so, the petioles to 2 mm long; blades oblanceolate to oblong, rarely narrowly linear, 15–70 mm long, 5–20 mm wide, the bases attenuate, tapering to a brief petiole, the apices rounded to acute, occasionally thickened to a minute apiculate tip; upper blade surfaces deep green, conspicuously black glandular punctate when dry, the glandular hairs orange when fresh, interspersed with minute, fine, whitish soft hairs, the venation not prominent; lower blade surfaces white tomentose, thickly invested with minute, fine, soft pointed hairs interspersed with black glandular trichomes, generally denser than on the upper surface, the midvein raised, red-brown, visible against the white indument. *Flowers* solitary, rarely 2, axillary, mostly appearing at the distalmost nodes of the branchlets; pedicels 2–12 mm long, erect to spreading, stout when short, filiform when long, bearing 2 linear, caducous bracteoles 0.5–1.5 mm long at or near the base. Floral tubes (5–)6-merous, homomorphic, obovoid-turbinate in bud with 6 processes (appendages *sensu* Koehne) projecting outward from the bud at the sinuses of the calyx lobes; floral tubes campanulate at anthesis, 2.5–5 mm long excluding lobes, 2.5–5 mm wide at the mouth, coriaceous, whitish pubescent, with 6 strongly reflexed deltoid calyx lobes, the lobes 2–2.5 mm long, 1.5–3 mm wide at their base, slightly shorter to distinctly shorter than the subtending tube; appendages present between the lobes to varying

degrees as a result of greater or lesser fusion of the margins of adjacent lobes, mostly ca. 0.5–1 mm long; external surface of the flower and pedicel glandular-punctate and finely pubescent, sometimes suffused rose in color; internal surface glabrous, deep rose-purple. *Petals* 6, attached within the tube at the base of the calyx sinuses, bright rose-purple, obovate to broadly oblong, venation simple, the midvein thick, bearing 4 or 5 secondary veins, without anastomoses between the veinlets, 5.5–10 mm long, 4–7 mm wide, including a claw 0.25–1.5 mm long. *Stamens* (16–)18(–20), occasionally increased by splitting of a filament near its base to form a double stamen, or reduced by absence of 1 of an episepalous pair, 6 single stamens epipetalous, 12 paired stamens episepalous, the epipetalous ones higher in the tube than the episepalous ones at ca. three-fifths vs. two-fifths the length of the tube, often slightly shorter than the episepalous stamens; filaments slender, well exserted, deep rose-purple, ca. 10 mm long, frequently persistent in the fruiting floral tube; anthers bright yellow, bisporangiate, dorsifixed medianly with a slender connective, strongly revolute at dehiscence, caducous. *Pollen* prolate-spheroidal, tricolporate, with three faint pseudocolpi; colpi meridionally elongated, equatorially arranged, equidistant, straight, 10–16 μm long, extending to within 3 μm of the pole, tapering to an acute apex, the costae colpi narrow, ca. 1 μm wide; exine faintly scabrate, tectate, with an ektexine bridge frequently present over the pore; pseudocolpi shorter than the colpi, 7–9 μm long, represented by a thinner granulated exine; pore circular, at midpoint of the colpus, 2.5–3 μm in diam.; grain size 19–26 μm long (P) × 14–20 μm wide at the equator (E). *Ovary* 2- or 3-locular, globose, thick-walled at anthesis, deep red-purple with mixed white pubescent and black glandular-punctate apex, stipitate, the stipe ca. 1 mm long, 0.5–0.7 mm wide at anthesis, surrounded at the base by a narrow ring of nectariferous tissue; placentation axile, the placenta swollen, fleshy, nearly globose; septa incomplete at the apex of the ovary; ovules numerous in each locule, attached over the entire placental surface, anatropous, erect; style red-purple, well exserted, 7–15 mm long, distinctly longer than the stamens, narrowing to the apex; stigma punctate, no wider than or only slightly wider than the narrowed apex of the style. *Capsule* exceeding the persistent floral tube by 2–3 mm at maturity, dry-walled, red-brown, septifragal marginicidally dehiscent from the apex for ca. one-half the length. Seeds numerous, deltoid- to cuneate-compressed, the chalazal end broadest, 1.2–1.3 mm long, 0.9–1.0 wide, the cotyledons flat, not revolute.

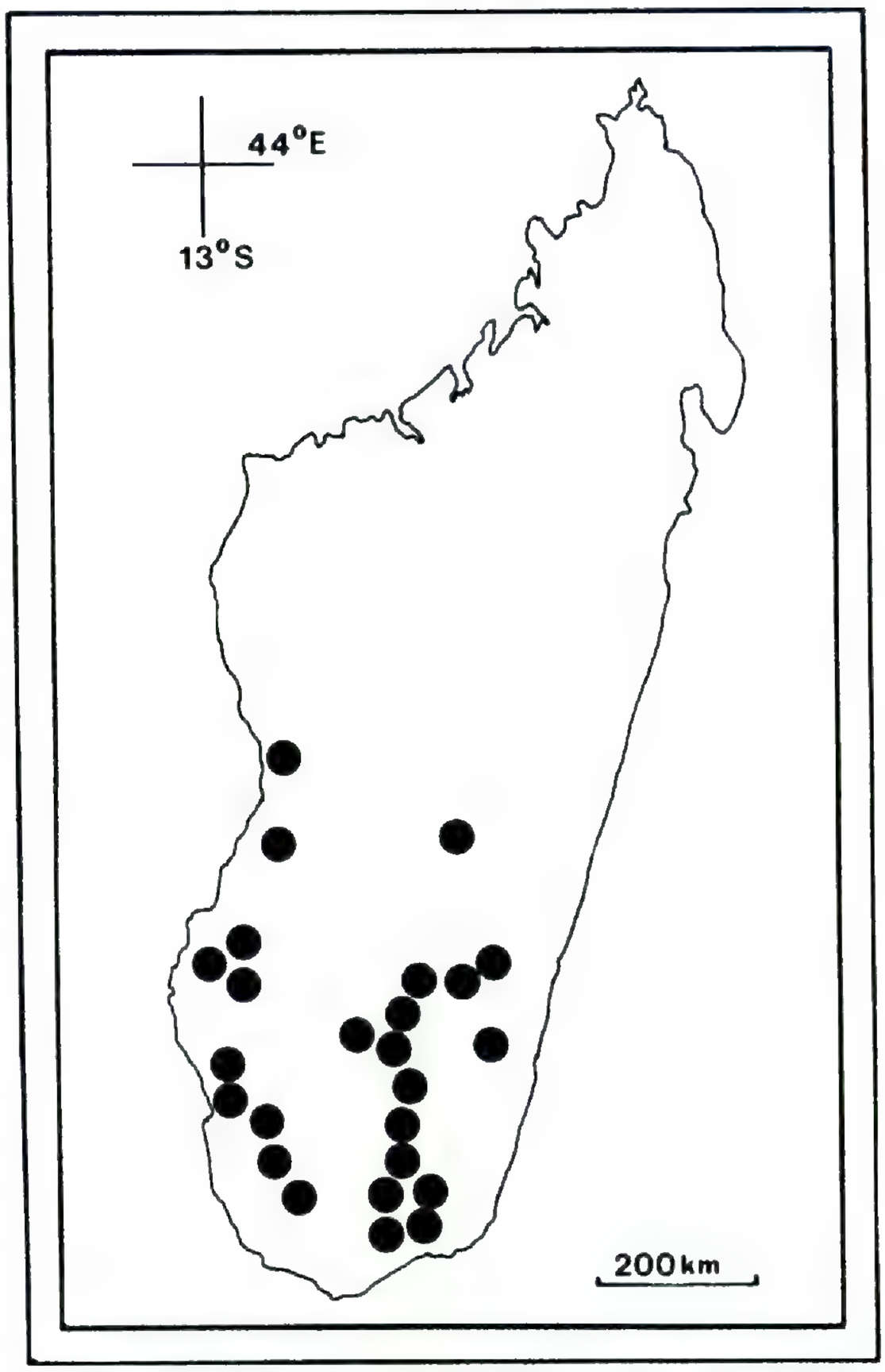


FIGURE 31. Distribution of *Koehneria madagascariensis* in Madagascar.

Common names. Pisopiso and Kipisopiso, meaning "cat-cat," used by the Bara tribe, who find the flowers of the plants pretty, just as they find cats pretty (Rakotozafy, pers. comm. to Dorr); Hazobotsy, meaning "white wood," also used by the Bara tribe (Dorr, pers. comm.).

Phenology. Flowering peaks approximately from late June to September, beginning prior to appearance of the new season's leaves. However, some flowering occurs virtually all year, depending on local conditions, the flowers then borne with current season's leaves. Capsule maturation beginning in August; seeds freely dispersed, with empty capsules persistent until the next flowering period.

Distribution. (Fig. 31.) Savannahs of semi-arid western and southern Tuléar Province and

bases of the central-south mountains in Fianarantsoa Province; in open grasslands and dry thickets on red calcareous soils, at altitudes of 100 to 800 m (Perrier de la Bâthie, 1954). These areas are characterized by a distinct dry season (six months or more) that is most prolonged in the southwest. Rainfall is irregular, between 500 and 1,000 mm per year, but less than 500 mm in the southwest. Mean temperature of the coldest month is 20°C (Koechlin et al., 1974). Specimens studied are cited below by phytogeographic province following Humbert (1955) and then alphabetically by collector.

Specimens examined. *Est:* Dist. Farafangana, Antahambohobe-Ivohibe, *Rakotovao s.n. (Réserves Naturelles 8102)* (TAN); Antahambohobe-Ivohibe, without collector (*Service des Eaux et Forêts 1945*) (TAN). *Centre:* Mahabo, *J. Bosser 9749* (TAN); 75 km sud de Betroka, *J. Bosser 13943* (TAN); Tsivory, *Catat 4358* (P); Common in the valleys to east of Ihosy, *W. Deans Cowan s.n.* (BM); 9 km N of Ihosy, *W. D'Arcy & A. Rakotozafy 15317* (MO); Domaine du centre moyen, au sud d'Ambalavao, *B. Descoings 977* (MO); Environs d'Ihosy, *B. Descoings 2775* (TAN); R. N. 7, P. K. 541, near La Brioche and 23 km S of the crossing of the Zamandao River, *L. J. Dorr 3923* (MO); R. N. 14, 36.1 km S of junction of R. N. 13 and R. N. 7, *L. J. Dorr 3933* (MO); 'Est d'Ihosy, *H. Humbert 4897* (BM); Haute Mananara, près poste forestier d'Imonty (Ambatohaly), *M. Keraudren 1519* (KE-Graham, P); Ihosy, montée vers l'Horombe, *J. & M. Peltier 2764* (TAN); Zazafotsy, Réserve 11, *Euphorbia* forest, *A. Richard 0114* (K). *Ouest:* Befandriana-Sud, 150 m, *O. Appert 40* (K, MO); Precise locality unknown, chiefly in Betsileo-land, *R. Baron 261* (K); Ambalavao, *J. Bosser 3578* (TAN); Nord de Belo Sur Tsiribihina, forêt tropophile, *J. Bosser 18134* (MO); Ranohira, *W. Rauh 10410* (TAN); between Beraketa and Antanimora, *W. D'Arcy & A. Rakotozafy 15320* (MO); Ambatofinandrahana, *P. Morat 126* (TAN); N. de Belo (Ouest), forêt sèche, *P. Morat 139* (TAN); Horombe, *P. Morat 2211* (MO); Ankilivalo (Ankazoabo) en savane, *P. Morat 2525* (TAN); Plateau de Bemaraha, without collector, *Herb. Jard. Bot. Tananarive 6154* (MO); Ampandrandava pas Betioky, without collector, *Herb. Jard. Bot. Tananarive 5111* (TAN). *Sud:* Ouest d'Ejeda, *J. Bosser 229* (MO); Imanombo, *Bosser 3877* (MO); Ifotaka, *J. Bosser 4029* (MO); Environs de Tuléar, *F. Chauvet 300* (KE-Graham, P); Androy, *R. Decary 2607* (US); Antanimora, *R. Decary 2935, 9198* (TAN); Behara, without collector (*Réserves Naturelles 2689*) (K, TAN); Tranomoro, *R. Decary 9013* (TAN); Environs Tuléar, *Dequaire 27541* (KE-Graham, P); Sud, without precise locality, *B. Descoings 542* (TAN); Bas Mangoky, *B. Descoings 778* (TAN); Vallée Moyenne du Mandrare près d'Anadabolava, *H. Humbert 12437* (KE-Graham, P, TAN, US); Rt. Nationale no. 7 at 63 km NE of Tuléar, *D. Lorence 1923* (MO); Tuléar, *A. Rakotozafy 767* (TAN); Behara, Amboasary, *Tsilizy s.n.* (*Réserves Naturelles 8338*) (TAN); Entre Antanimora et Betroka, *Ursch s.n.* (TAN); Ampanihy, route Ejeda, without collector, *Herb. Jard. Bot. Tananarive 4217* (TAN). Without precise locality or collector, (*Herbier de la station agricole de l'Alaotra 4615, 24086*) (MO).

The genus is showy in bloom, with the large bright rose petals extending well beyond the shorter floral tube, and the flowers scarcely obscured by the elongate leaves, which are not fully developed at first flower appearance. The plant is widely distributed on the drier side of the island and is still quite common in the south-central area and the southwest. At the time of its original discovery, it was reportedly very common in the type area, where it grew with the equally abundant *Woodfordia fruticosa* (Baker, 1882).

The tribal position of *Koehneria* is not specified because tribal limits in the family were erected on an erroneous distinction between complete septal development (*Nesaeeae*) and incomplete septal development (*Lythreae*). Tobe (in prep.) has found that, in fact, all genera are characterized by incomplete septal development. Studies in wood anatomy and palynology support the interpretation that there is no major natural division in the family corresponding to the present tribes (Baas & Zweypfenning, 1979; Lee, 1979).

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WOOD ANATOMY OF LYTHRACEAE—ADDITIONAL GENERA (*CAPURONIA, GALPINIA, HAITIA, ORIAS,* AND *PLEUROPHORA*)[1,2]

PIETER BAAS[3]

ABSTRACT

The wood anatomy of the lythraceous genera *Capuronia* (Madagascar), *Galpinia* (South Africa), *Haitia* (Hispaniola, Dominican Republic), *Orias* (= *Lagerstroemia excelsa* from China), and *Pleurophora* (South America) is described as an addendum to earlier studies on the wood anatomy of the family. *Capuronia* and *Galpinia* resemble each other and the genera *Pehria* and *Ginoria* very closely in their wood structure. The resemblance to the last two genera is contrasted by major differences in morphological features and may be due to parallel development. *Haitia* resembles *Lafoensia* and *Tetrataxis* in its wood anatomy, but also shows similarities with *Ginoria* p.p. The wood anatomy of *Orias* supports its modern treatment as *Lagerstroemia excelsa,* and shows much resemblance to that of *Lagerstroemia subcostata. Pleurophora* shows a striking wood anatomical similarity with *Heimia,* but taking into account characters from reproductive morphology, this similarity seems to be due to parallel evolution, despite the very different ecologies of the two taxa. *Pleurophora* may be more closely allied to *Woodfordia,* with which it also shares a number of wood anatomical characters. The likelihood of parallel development of chambered crystalliferous fibers and vascular tracheids in the evolution of the Lythraceae is discussed, and an earlier phylogenetic classification of the family based on wood anatomy is modified to a purely phenetic scheme, not necessarily indicating mutual affinities.

In an earlier study a broad survey of the wood anatomy of the Lythraceae was presented (Baas & Zweypfenning, 1979). Together with studies on the genera *Alzatea* (Baas, 1979), *Punica* (Bridgwater & Baas, 1978), and *Koehneria* (Graham et al., 1986), this left only the woody genera *Capuronia, Galpinia, Haitia, Orias* (now *Lagerstroemia*), and *Pleurophora* as taxa whose wood anatomy was unknown. Thanks to the help of Peter Raven (Missouri Botanical Garden) and several other botanists, vouchered wood samples have recently become available for study. This paper thus completes the wood anatomical survey of the family at the generic level. There is still scope for substantial extension of wood anatomical studies below the genus level, because many genera show an interesting wood anatomical range that can aid in arriving at more natural classifications. Four genera without truly woody representatives, viz. *Didiplis, Hionanthera, Peplis,* and *Rotala* are of course beyond the scope of this study.

Methods employed are similar to those of the earlier studies and the descriptive style more or less follows the same format, with the exception that for material from thin stems full quantitative characters are presented here. It should be stressed that these values can be taken only as a very rough indication of what the values in thicker stems might be. As is generally known, vessel diameter, vessel member length, fiber length, and ray width increase from the pith outward in juvenile wood, while vessel frequency decreases. Moreover, the rays in juvenile wood usually have a much higher proportion of strongly upright cells than mature wood.

All wood samples and slides studied are kept at the Rijksherbarium (L_w). When known, the location of the herbarium vouchers is indicated under material studied using the abbreviations from Index Herbariorum.

WOOD ANATOMICAL DESCRIPTIONS AND TAXONOMIC NOTES

CAPURONIA LOURTEIG (FIGS. 1–3)

Material studied: *C. madagascariensis* Lourteig: Madagascar, *Dorr et al. 4136* (twig of 6 mm

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[1] The other genera were described in Baas and Zweypfenning (1979), Bridgwater and Baas (1978), and Graham et al. (1986).

[2] I am greatly indebted to P. Raven (Missouri Botanical Garden, St. Louis) for his stimulating role in obtaining material for this study. Thanks are also due to T. A. Zanoni (Jardin Botanico Nacional, Dominican Republic), P. Hoch (Missouri Botanical Garden), B. de Winter (Botanical Research Institute, Pretoria, South Africa), and C. L. Cristóbal (Corrientes, Argentina) for supplying wood samples. Discussions in correspondence with S. A. Graham (Kent State University, Ohio) and H. Tobe (Chiba University, Japan) have been most helpful for arriving at the conclusions presented here.

[3] Rijksherbarium, P.O. Box 9514, 2300 RA Leiden, The Netherlands.

diam. with many indistinct growth increments, MO), *Léandri 2669* (twig of 2.5 mm diam. with 7 growth increments, L), *Bernardi 11425* (twig of 3.5 mm diam. with 5 growth increments, L).

Shrub in dry tropical forests, West Madagascar.

Growth rings faint to distinct. *Vessels* diffuse or wood weakly semi-ring-porous. Vessels ca. 200–300 per square mm, ca. 30% solitary, the remainder in radial (rarely oblique to tangential) multiples of 2–4(–6), sometimes including very narrow vessel elements, round to weakly angular, tangential diam. (20–)30–35(–45) μm, radial diam. up to 50 μm, walls 2–6 μm thick. Perforations simple in oblique end walls. Vessel member length (130–)210–240(–380) μm. Intervessel pits alternate, vestured, round to weakly polygonal, 4–6 μm. Vessel-ray pits similar but half-bordered. Vessels occasionally with gummy contents. Spiral thickenings absent. *Fibers* thin- to medium thick-walled, or thick-walled and gelatinous, (220–)340–390(–560) μm long, with simple to minutely bordered pits mainly confined to the radial walls, septate, partly chambered crystalliferous, mostly with cytoplasmic contents. *Parenchyma* extremely scanty paratracheal, in 3–4-celled strands. *Rays* ca. 16 per mm, exclusively uniseriate, (1–)3–6(–20) cells high, composed of upright to weakly procumbent cells (juvenilistic to Kribs' heterogeneous type I). *Crystals* solitary prismatic, large and one per chamber in crystalliferous fibers, sometimes associated with a number of minute, irregularly shaped crystals. Silica bodies absent.

Taxonomic note. When Lourteig (1960) described the genus *Capuronia* she considered it close to the genus *Nesaea* of Koehne's subtribe Nesaeinae (1892). Other genera in this subtribe with woody species are *Adenaria, Crenea, Decodon, Ginoria, Heimia, Pehria,* and *Tetrataxis. Haitia* would also belong there (see below). In its wood anatomy *Capuronia* resembles *Galpinia, Ginoria,* and *Pehria* rather than *Nesaea.* The former genera as well as *Punica* (a putative Lythraceae or Punicaceae, cf. Bridgwater & Baas, 1978) share chambered crystalliferous fibers, a character that was considered to be strongly indicative of mutual affinity (Baas & Zweypfenning, 1979). *Capuronia* and *Galpinia* share the presence of foliar nectaries but differ substantially in floral and pollen morphology (Graham, pers. comm.). Both Graham and Tobe (pers. comm.) consider *Ginoria, Pehria,* and *Punica* at most distantly related to *Capuronia.* This might indicate that chambered crystalliferous fibers have evolved independently in at least two different groups of genera of the Lythraceae.

A wood anatomical comparison of *Capuronia* and *Galpinia* yields as the only relevant difference the exclusively uniseriate rays of the former and the uni- and biseriate rays in the latter. This is a very minor difference, especially because biseriate rays are quite rare in *Galpinia* and because the possibility cannot be excluded that *Capuronia* is capable of forming some biseriate rays in more mature wood.

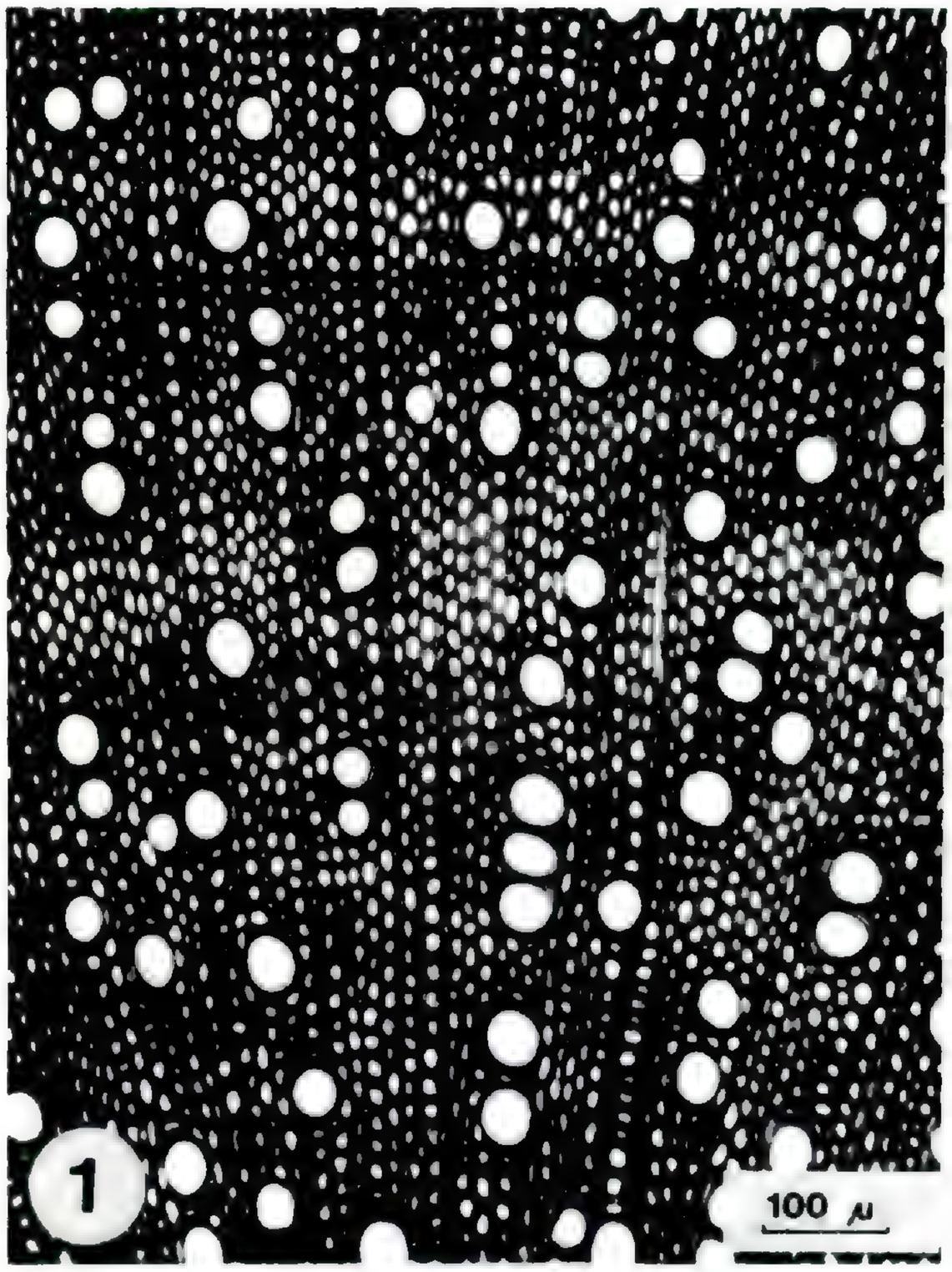
GALPINIA N.E. BR. (FIGS. 4–6)

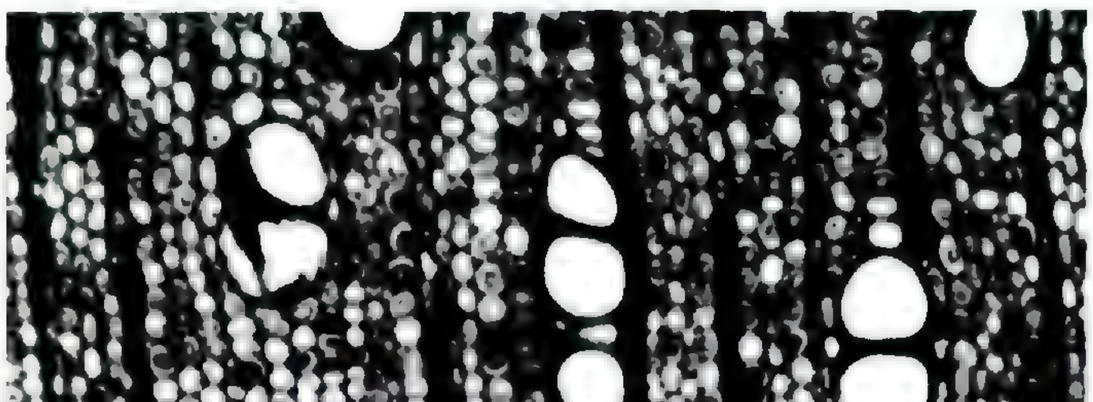
Material studied: *G. transvaalica* N. E. Br., South Africa, *Balsinhas 3636* (stem of 3 cm diam., PRE).

Shrubs or small trees in rather open mountain vegetation.

Growth rings faint to distinct. Wood diffuse- to weakly semi-ring-porous. *Vessels* ca. 140 per square mm, ca. 20% solitary, remainder in radial multiples of 2–5(–10), occasionally in clusters including very narrow vessels, weakly angular, tangential diam. (20–)40(–60) μm, radial diam. up to 65 μm, walls 2–4 μm thick. Perforations simple in oblique to nearly horizontal end walls. Vessel member length (300–)390(–500) μm. Intervessel pits alternate, vestured, round to polygonal, 5–7 μm. Vessel-ray pits similar but half-bordered. Some vessels with gummy contents. Spiral thickenings absent. *Fibers* thin- to medium thick-walled or thick-walled and gelatinous, (390–)580(–720) μm long, with simple pits mainly confined to the radial walls, septate, partly chambered crystalliferous; non-crystalliferous fibers rich in starch grains. *Parenchyma* extremely scanty paratracheal, in 2-celled strands, intergrading with wide, septate paratracheal fibers. *Rays* ca. 17 per mm, mainly uniseriate, partly with a low biseriate central part, (1–)2–8(–20) cells high, heterocellular, composed of upright and square to procumbent cells (Kribs' heterogeneous types I–II). *Crystals* solitary prismatic or irregularly shaped, one to several per chamber in crystalliferous fibers. Silica bodies absent.

Taxonomic notes. Galpinia was doubtfully placed in an alliance with *Diplusodon* and *Pemphis* (Diplusodontinae in Koehne's classification, 1892) by Brown (1894) when he described this monotypic genus from South Africa. Koehne





FIGURES 1–6.—1–3. *Capuronia madagascariensis*.—1. TS.—2. TLS, note septate fibers.—3. RLS, note chambered crystalliferous fibers.—4–6. *Galpinia transvaalica*.—4. TS.—5. TLS, note septate fibers.—6. Maceration, chambered crystalliferous fiber.

(1903) followed this suggestion but also commented on the resemblance in habit to *Lawsonia* and *Lagerstroemia.*

The main wood anatomical difference between *Galpinia* and *Diplusodon* lies in the nonseptate, noncrystalliferous fibers of *Diplusodon. Pemphis* is wood anatomically quite isolated within the family on account of its well developed vasicentric parenchyma (Baas & Zweypfenning, 1979) and differs in many other wood anatomical characters from *Galpinia.* In contrast, there are very close wood anatomical similarities between *Galpinia* and *Capuronia, Ginoria, Pehria,* and *Punica.* On the basis of morphological characters (Graham, pers. comm.) only a close affinity with *Capuronia* seems to be supported.

HAITIA URBAN (FIGS. 7, 8)

Material studied: *H. pulchra* Urban & Ekman, Haiti, *Zanoni et al. 28433* (stems of 2, 3, and 4 mm diam., MO).

Shrubs of dry limestone terraces.

Growth rings faint to absent. *Vessels* diffuse, ca. 100 per square mm, 15% solitary, remainder in radial (to oblique) multiples of 2–4(–5), rounded to angular, tangential diam. (20–)40 (–50) μm, radial diam. up to 60 μm, walls 1.5–3 μm thick. Perforations simple in oblique end walls. Vessel member length (300–)390(–500) μm. Intervessel pits alternate, vestured, round to polygonal, 4–7 μm. Vessel-ray pits similar but half-bordered. Spiral thickenings and vessel contents absent. *Fibers* thin- to medium thick-walled or thick-walled and gelatinous, (390–)580(–720) μm long, with simple pits mainly confined to the radial walls, septate. *Parenchyma* very scanty paratracheal, in 2–3-celled strands. *Rays* ca. 13 per mm, 1–2(–3)-seriate, (1–)2–12(–24) cells high, heterocellular with strongly upright marginal cells and (in case of taller rays only) square to procumbent central cells (Kribs' heterogeneous type I). *Crystals* and silica bodies absent.

Taxonomic note. Haitia was described by Urban (1919) as a relative of the genus *Ginoria.* Graham (pers. comm.) supports this affinity, but wood anatomically *Haitia* is closer to *Tetrataxis* and *Lafoensia* (cf. Baas & Zweypfenning, 1979). There is a perfect wood anatomical match especially with *Tetrataxis* from Mauritius. Interestingly enough, Koehne (1886) assumed phylogenetic links between *Tetrataxis* and *Ginoria* so that in an indirect way wood anatomy is not entirely in conflict with a presumed affinity of *Haitia* with *Ginoria.* Graham and Lorence (1978) concluded, however, that the relationships of *Tetrataxis* to other members of the Lythraceae remains unknown, thus invalidating this argument.

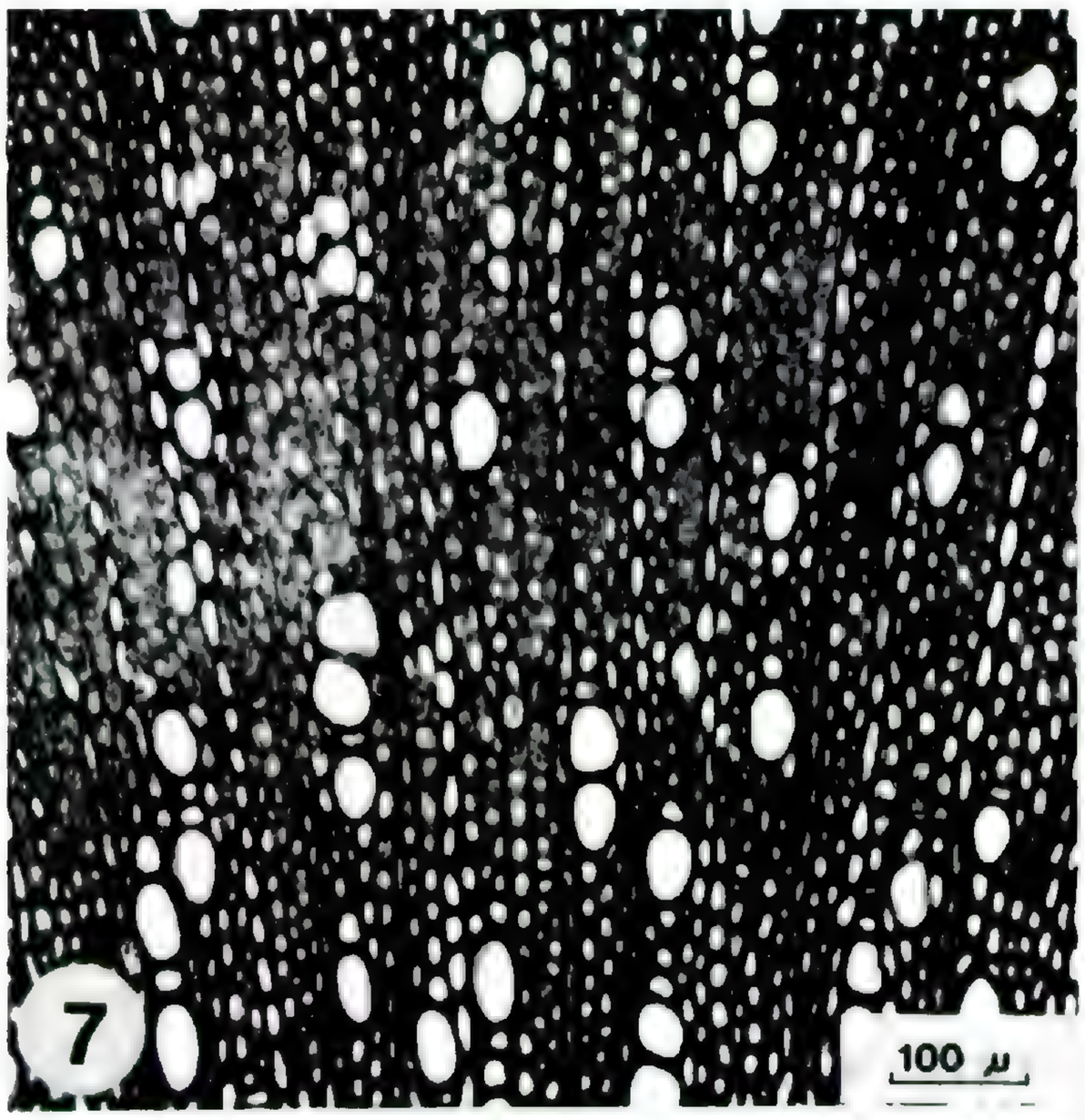
The main difference between *Ginoria* and *Haitia* concerns the chambered crystalliferous fibers in the former, which are absent from *Haitia.* However, in the restricted material of *Ginoria,* we also encountered one specimen (of *G. americana*) that was devoid of crystalliferous fibers (Baas & Zweypfenning, 1979). Studies of more materials of *Ginoria* and *Haitia* might thus reveal a wood anatomical overlap between the two genera, since they are similar in most other wood anatomical features.

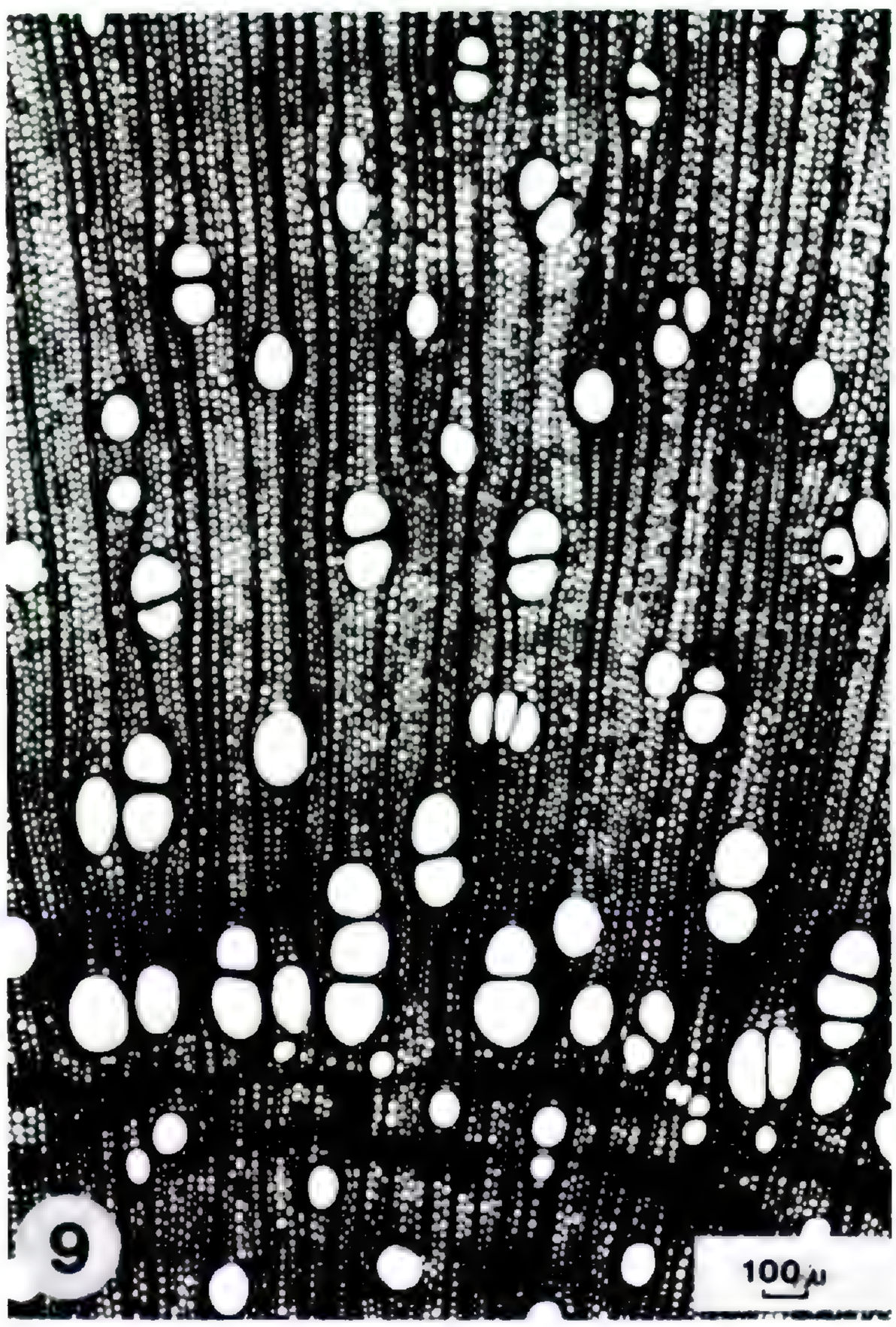
ORIAS DODE (FIGS. 9, 10)

Material studied: *Lagerstroemia excelsa* (Dode) Chun ex S. Lee & L. Lau (= *Orias excelsa* Dode), China, Sichuan, *Liu et al. 5220* (stem of ca. 2 cm diam., MO).

Trees, in rainforests between 1,200 and 2,000 m.

Growth rings distinct. Wood semi-ring-porous. *Vessels* ca. 28 per square mm, 35% solitary, remainder in radial multiples of 2–3 or in small clusters, round to oval, tangential diameter (30–)75(–120) μm, radial diam. up to 160 μm, walls 2–5 μm thick. Perforations simple in horizontal to oblique end walls. Vessel member length (200–)300(–360) μm. Intervessel pits alternate, vestured, round to polygonal, 6–8 μm. Vessel-ray pits and vessel-parenchyma pits alternate to reticulate, with reduced borders to simple, infrequently unilaterally compound or elongate. Thick-walled tyloses present in some of the vessels. Vessel contents or spiral thickenings absent. *Fibers* of two types: 'normal' fibers with simple pits mainly confined to the radial walls, thin- to medium thick-walled, (280–)520 (–740) μm long; and 'parenchyma-like' fibers, all thin-walled, 200–400 μm long, and also with simple pits mainly in the radial walls, in poorly defined broad tangential, discontinuous bands, including some true parenchyma strands. Both types of fibers septate and partly chambered crystalliferous. *Parenchyma* scanty paratracheal and scattered between the 'parenchyma-like' fibers, in 2–5-celled strands. *Rays* ca. 16 per mm, almost exclusively uniseriate, rarely with a low biseriate portion, (1–)2–8(–20) cells high, weakly





FIGURES 7–10.—7, 8. *Haitia pulchra.*—7. TS.—8. TLS, note septate fibers and heterocellular rays.—9, 10. *Lagerstroemia excelsa.*—9. TS, note faintly expressed fiber dimorphism.—10. TLS, 'normal' fibers on the left and thin-walled 'parenchyma-like' fibers on the right (including some chambered crystalliferous fibers).

heterocellular with one row of square to weakly upright marginal cells or completely composed of procumbent cells (Kribs' heterogeneous type III to homogeneous). *Crystals* solitary prismatic, large and one per chamber or accompanied by smaller crystals of irregular shape, in crystalliferous fibers. Silica bodies absent.

Taxonomic note. *Lagerstroemia excelsa* was originally described as *Orias excelsa* by Dode (1909), who noted that it was close to *Lagerstroemia* and *Lawsonia* (subtribe Lagerstroeminae). In the flora of China, *Orias* was reduced to *Lagerstroemia* by Lee and Lau (1983) and *L. yangii* was recognised as a synonym. Dode (1909) and Furtado and Srisuko (1969) stressed affinities of this species with *L. subcostata.*

Wood anatomically *L. excelsa* fits very well into the group of *Lagerstroemia* species with fiber dimorphism. This group also includes *L. subcostata.* The wood anatomical differences between *L. excelsa* and *L. subcostata* are very slight: in the limited material of the latter species studied only its diffuse-porosity and more prominently half-bordered vessel-ray pits contrast with the situation in *L. excelsa* (cf. Baas & Zweypfenning, 1979). Other *Lagerstroemia* species with fiber dimorphism are *L. calyculata, L. floribunda, L. indica, L. loudonii,* and *L. tomentosa* and probably a number of other species that have hitherto never been described wood anatomically.

PLEUROPHORA DON

Material studied: *P. patagonica* Spegazzini, Argentina, *Grondona 23859* (stem of ca. 8 mm diam. with 14 annual rings, MO); *P. saccocarpa* Koehne, Argentina, *Schinini & M. Martinez Crovetto 22640* (stems of 3 and 5 mm diam., swollen stem base of 8 mm diam., root of 1.5 mm diam., MO).

Fruticose or herbaceous perennials or annuals of dry places.

In view of the substantial wood anatomical differences between the two species studied, separate descriptions are given for each.

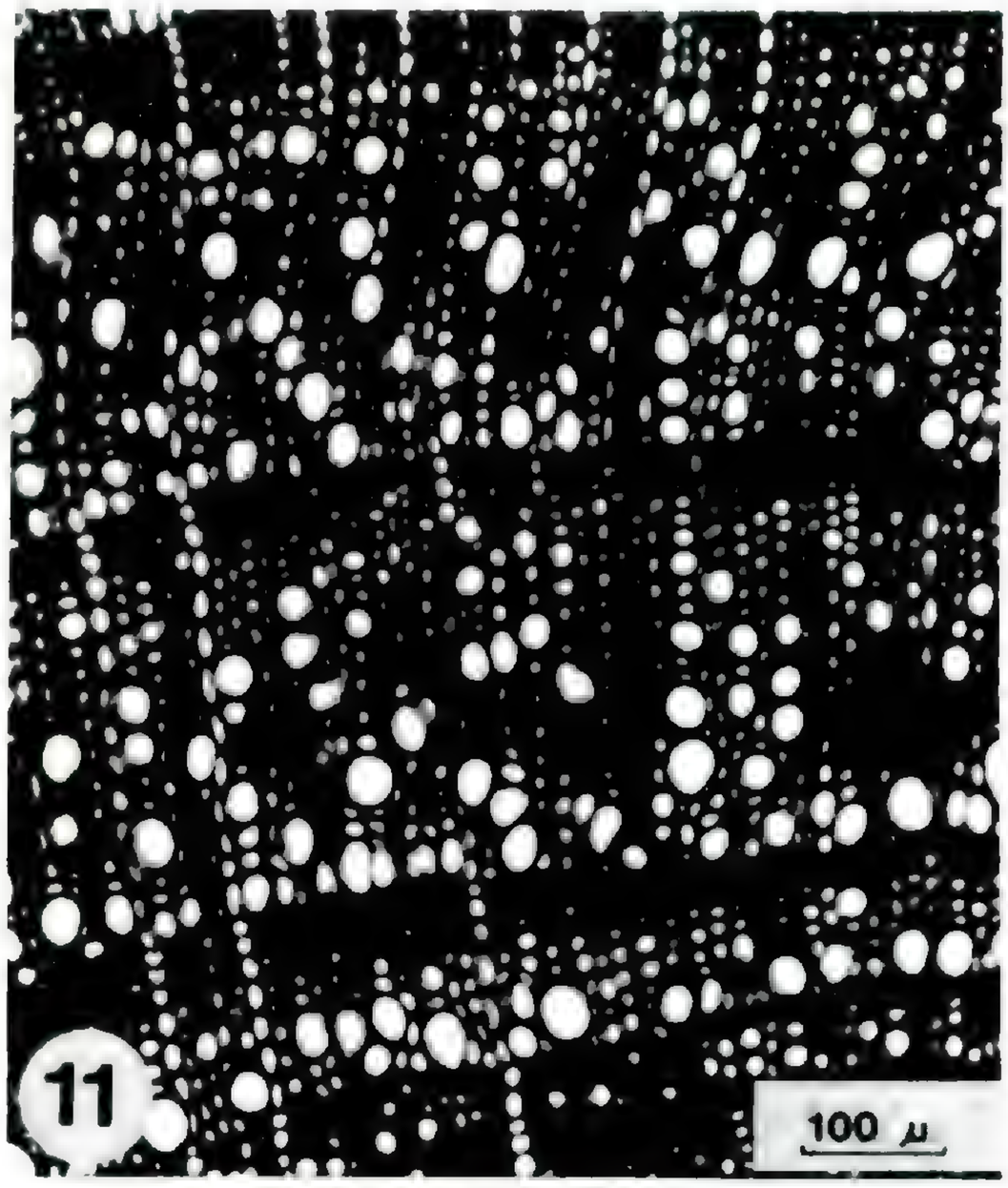
P. patagonia (Figs. 11–13)

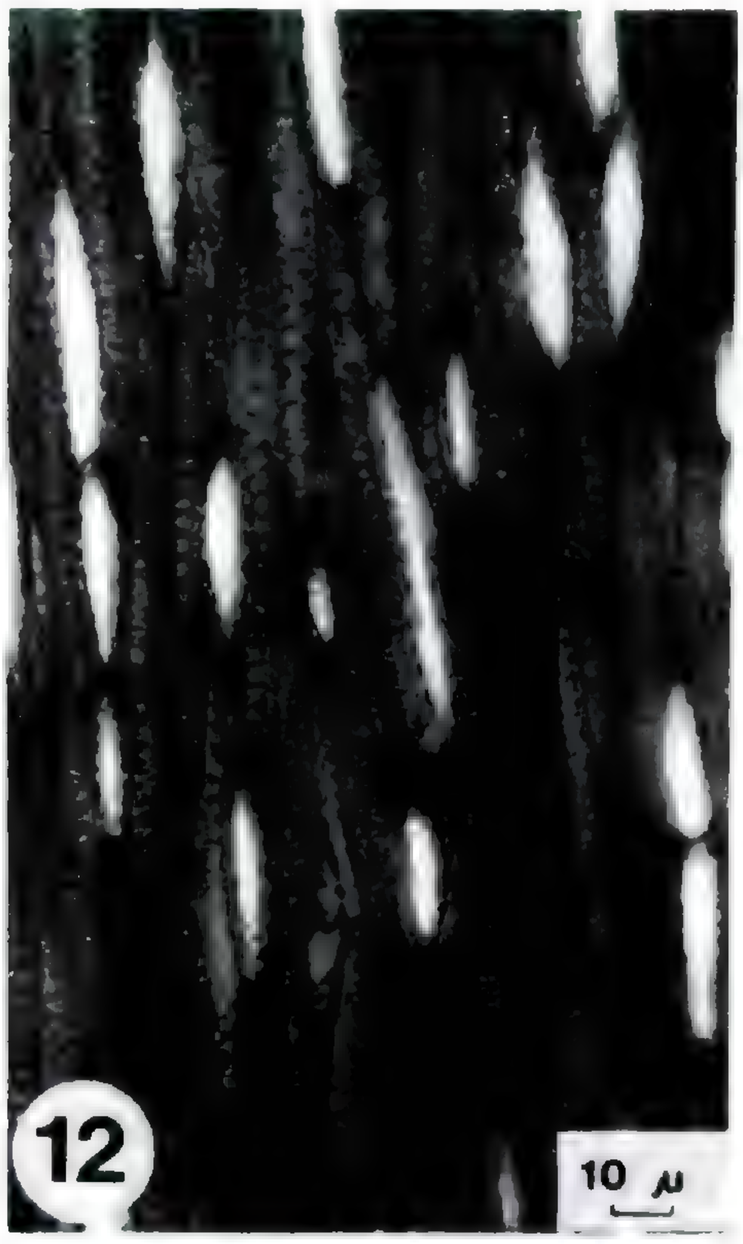
Growth rings distinct. Wood semi-ring-porous. *Vessels* ca. 250–500 per square mm, mainly in multiples (radial, oblique or tangential; the extent of the multiples is difficult to estimate due to intergradation of narrow vessels and vascular tracheids in the latewood), vessels rarely solitary, rounded to slightly angular, tangential diam. (10–)20(–30) μm, radial diam. up to 40 μm, walls 2–3 μm thick. Perforations simple in oblique end walls. Vessels of two types: 'normal' ones, and very narrow ones intergrading with vascular tracheids in the latewood. Length of 'normal' vessel members (150–)200(–250) μm; of the very narrow vessel members and vascular tracheids (170–)215(–300) μm. Intervessel pits alternate, vestured, polygonal to rounded, 3–7 μm. Vessel-ray pits similar but half-bordered. All vessels and vascular tracheids with closely spaced spiral thickenings. Some vessels with dark-staining gummy contents. *Vascular tracheids* (see above) forming the ground tissue in the latewood, thick-walled. *Fibers* thin- to medium thick-walled, forming ground tissue in the early and intermediate wood only, (210–)285(–360) μm long, with simple to minutely bordered pits mainly confined to the radial walls, nonseptate, mostly with cytoplasmic contents. *Parenchyma* virtually absent; only one 2-celled paratracheal strand noted. *Rays* ca. 12 per mm, exclusively uniseriate and very low, 1–8 (mostly only 1–2) cells high, entirely composed of upright cells. *Crystals* and silica bodies not observed.

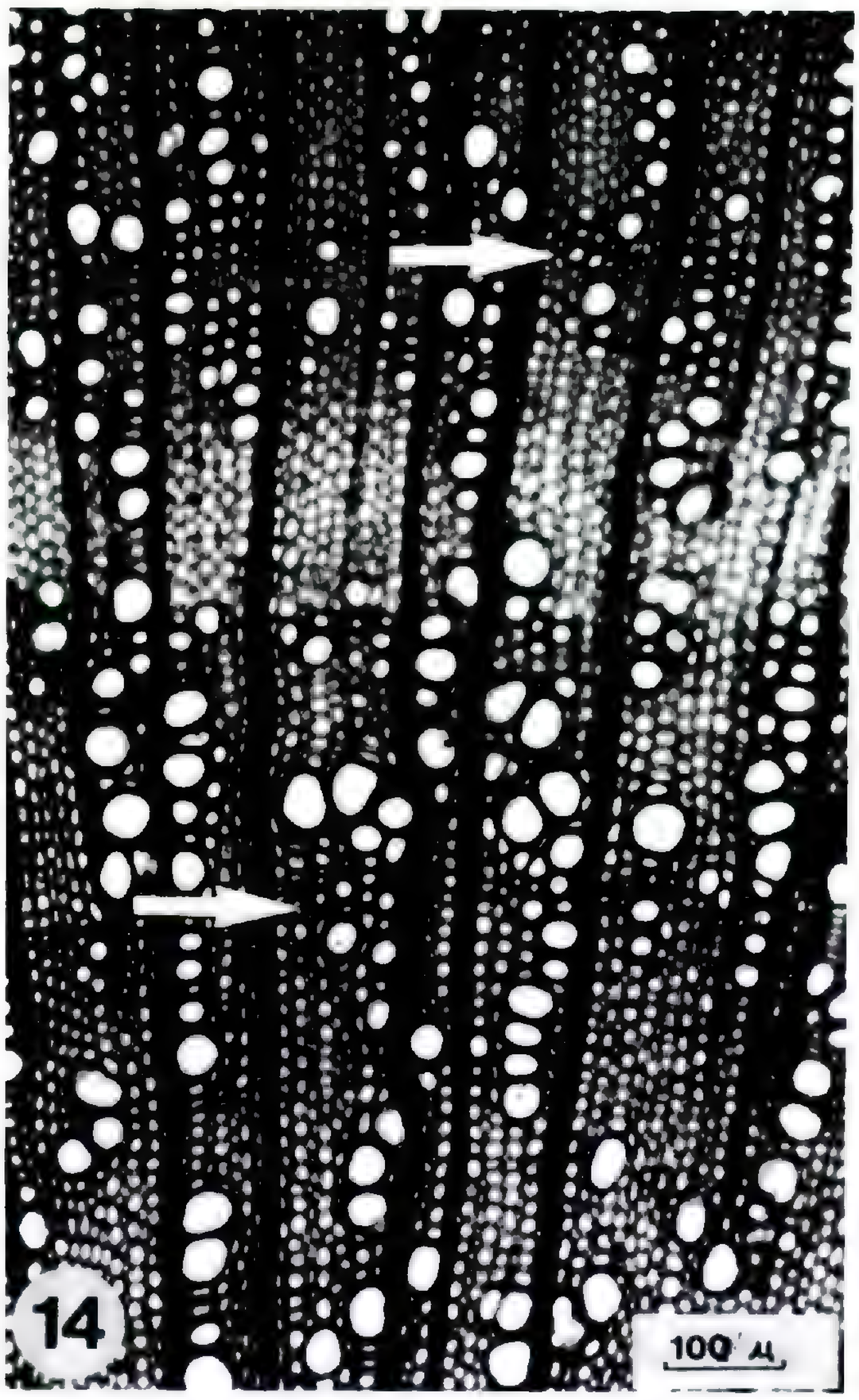
P. saccocarpa (Figs. 14–16)

The various parts of stems and root do not differ substantially from each other; the description is based on the stem of 5 mm diameter.

Growth rings faint to distinct. Wood diffuse- to semi-ring-porous. *Vessels* ca. 400 per square mm, mainly in radial multiples of 2–6(–10), rarely solitary or in short oblique to tangential multiples, rounded to slightly angular, tangential diam. (10–)20(–40) μm, radial diam. up to 45 μm, walls 1–4 μm thick. Perforations simple in oblique to nearly horizontal end walls. Vessels of two types: 'normal' ones, and very narrow ones intergrading with vascular tracheids associated with vessel multiples and in zonate bands coinciding with growth ring boundaries. Length of 'normal' vessel members (150–)235(–350) μm, of the very narrow vessel members and vascular tracheids (180–)260(–360) μm. Intervessel pits alternate, vestured, round to polygonal, ca. 6 μm. Vessel-ray pits similar but half-bordered. Spiral thickenings absent. Some vessels with dark-staining contents. *Vascular tracheids* (see above) forming ground tissue of narrow tangential bands associated with growth ring boundaries (but not







FIGURES 11–16. *Pleurophora*.—11–13. *P. patagonica*.—11. TS, note latewood zones of thick-walled tracheids.—12. TLS through latewood. Note low rays and tracheids with spiral wall thickenings.—13. Maceration, part of vessel element with spiral thickenings.—14–16. *P. saccocarpa*.—14. TS. Arrows indicate indistinct zones with tracheids.—15. TLS, note relatively tall rays.—16. Maceration, vessel element with smooth wall.

always identifiable as latewood), thick-walled. *Fibers* thin-walled or thick-walled and gelatinous, (240–)350(–480) μm long, with simple to minutely bordered pits mainly confined to the radial walls, mostly nonseptate, very rarely septate, often with cytoplasmic contents and starch grains. *Parenchyma* absent. *Rays* ca. 24 per mm, exclusively uniseriate, (1–)2–10(–25) cells high, largely composed of upright cells, but some with square to procumbent cells in part of the rays. *Crystals* and silica bodies not observed.

Taxonomic note. *Pleurophora saccocarpa* differs from *P. patagonica* in its lack of spiral vessel- and tracheid wall thickenings and its much greater ray height. *Pleurophora patagonica* is really very unusual in exhibiting such very low rays, so far found nowhere else in the Lythraceae. In other wood anatomical features the two species are quite similar. Their most striking feature is in the occurrence of bands of (vascular) tracheids.

Koehne (1892) incorporated *Pleurophora* in the Lythrinae, a subtribe in which some genera include woody species: *Ammannia, Cuphea, Lythrum,* and *Woodfordia.* Tobe (pers. comm.) considers *Pleurophora* close to *Cuphea* but the latter genus lacks tracheids in its wood. Wood anatomically *Pleurophora patagonia* is strikingly similar to *Heimia,* through the shared vascular tracheids in the latewood and the prominent spiral thickenings in both vasacular tracheids and vessel members and similarities in all other wood features (cf. Baas & Zweypfenning, 1979; a mature wood sample of *Heimia myrtifolia* was also studied for the present comparison). *Pleurophora saccocarpa* is also quite similar to *Heimia,* but lacks spiral thickenings and has lower rays.

The only other genus in Lythraceae with numerous narrow vessels intergrading with vascular tracheids at growth ring boundaries is *Woodfordia,* a genus that in other wood anatomical characters is also similar to *Pleurophora.* Thus an affinity of *Pleurophora* to one of the members of the subtribe Lythrinae can be supported.

The similarities between the wood of *Heimia* and *Pleurophora* can be contrasted by numerous significant differences in floral and pollen morphology (Graham, pers. comm.; Koehne, 1903). Because of these differences a close mutual affinity seems unlikely and this makes it probable that the wood anatomical similarities are due to parallel evolution. This parallelism cannot be accounted for by similar selective pressure induced by environmental factors on the hydrosystem: *Heimia* is a genus of shrubs occurring along river margins and in wet ditches; *Pleurophora* is a genus of herbaceous and fruticose annuals and perennials of dry places.

Discussion

In an earlier paper a tentative phylogenetic classification of the Lythraceae was proposed based exclusively on wood anatomical diversity patterns (Baas & Zweypfenning, 1979). It would be quite easy to fit the genera described in this paper into this classification. However, assumptions on the monophyletic nature of chambered crystalliferous fibers and fiber-dimorphism, as well as classical transformation series for types of ray tissue according to Kribs (1935), played important roles in constructing this phylogenetic scheme. In the taxonomic notes for *Galpinia* and *Capuronia* it had to be concluded that on the totality of evidence from reproductive and vegetative morphology and wood anatomy, close affinities of these genera with *Pehria* and *Ginoria* are unlikely, which implies that their shared chambered crystalliferous fibers must have originated independently. The same conclusion probably applies to vascular tracheids in *Pleurophora,* which apparently arose independently from those in *Heimia.* Ray specialisation as already emphasised in the earlier paper (Baas & Zweypfenning, 1979) and later advocated in a more general context (Baas, 1982), is probably highly subject to parallelism and reversibility and cannot be used as an unambiguous criterion for determining advancement levels or mutual affinity. This is especially the case in the Lythraceae in which the wide range of habit categories (from annual herbs, via fruticose perennials to large trees) makes the developmental phase of the outer wood of a plant of small stature incomparable to that of a large tree. The distribution of septate and nonseptate fibers in *Cuphea* and *Pleurophora* (which both may or may not have septate fibers) also suggests parallel development or reversibility of these character states.

For the reasons outlined above, I refrain from using the data on *Capuronia, Galpinia, Haitia,* and *Pleurophora* for the elaboration of a *phylogenetic* classification of the Lythraceae. Instead the most important data on these genera are summarised together with those on other Lythraceae in a *phenetic* scheme (Fig. 17). Even as a phenetic scheme, Figure 17 cannot give an ideal picture

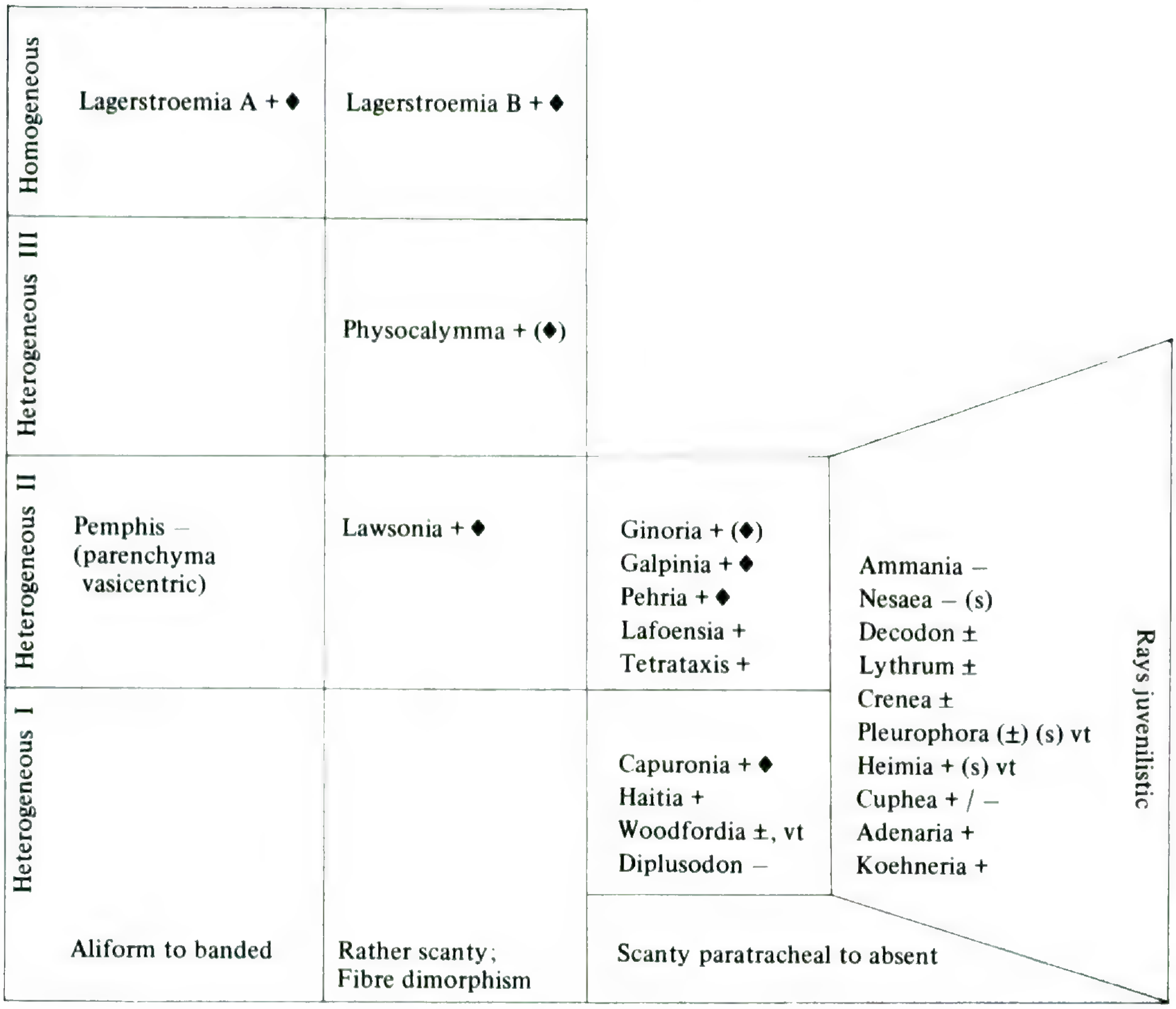


FIGURE 17. Grouping of Lythraceae genera on wood anatomical characters. Ray tissue characters (according to Kribs, 1935, 1968) on the vertical axis*; parenchyma characters on the horizontal axis. The column of genera on the right has juvenilistic rays composed mainly or exclusively of upright cells. Other wood anatomical characters indicated in the diagram: ◆: chambered crystalliferous fibers; +, ± and (±): septate fibers abundant, infrequent and present in only part of the specimens respectively; –: all fibers nonseptate; s: spiral thickenings present on the vessel walls; vt: vascular tracheids common; ( ): feature only present in part of the species or specimens.

* Within individual genera or even species or specimens two sequential ray tissue types may intergrade. In this diagram only the most frequently occurring type has been taken into account.

of the wood anatomical similarities and differences of some groups of genera. This is partly because of the limitations imposed by any two-dimensional diagram and because in the present scheme ray characters are given too much significance. Differences between two sequential ray types may be taxonomically very insignificant (cf. Baas & Zweypfenning, 1979) and yet they cause *Capuronia* to be in a different cluster of genera in Figure 17 from that of *Galpinia, Ginoria,* and *Pehria,* with which it has more in common than with *Haitia, Woodfordia,* and *Diplusodon.* Similarly, *Woodfordia,* although similar to *Heimia* and *Pleurophora,* figures in a different column because of relatively minor differences in ray composition. Therefore Figure 17 should be interpreted with caution and be seen as only one possible way to present the wood anatomical variation in the Lythraceae in an orderly manner.

There is no reason to abandon our earlier views that within Lythraceae the combination of heterogeneous type I (sensu Kribs) rays, septate fibers, and scanty paratracheal parenchyma presents the plesiomorphic condition for the family. Specialisation in rays towards homogeneity in

the tree genera on the one hand and towards juvenilism in small shrubs and fruticose perennials on the other hand, acquisition of vascular tracheids, spiral vessel wall thickenings, crystalliferous fibers, fiber dimorphism, and banded or vasicentric parenchyma, as well as loss of fiber septation in some taxa, all probably represent apomorphic character states. The likelihood that these apomorphic states evolved independently in some only remotely related Lythraceae became apparent in discussions with specialists of the family who are engaged in taxonomic and morphological studies of the family (S. A. Graham and Hiroshi Tobe). The problem at this stage is that we have no ways to identify in which combination of taxa the apomorphic state is monophyletic and in which it is not. It seems to me that further progress in interpreting the wood anatomical diversity in terms of character polarity and phylogenetic significance can be achieved only by extending our wood anatomical data base with many more species, and by active cooperation with taxonomists.

The extended generic survey of wood anatomy of the Lythraceae does not alter the wood anatomist's view of the position of the family within the order Myrtales (Van Vliet & Baas, 1984).

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NEW NEOTROPICAL SPECIES OF *MELIOSMA* (SABIACEAE)[1]

ALWYN H. GENTRY[2]

ABSTRACT

Meliosma hartshornii A. Gentry, from Costa Rica; **M. corymbosa** A. Gentry and **M. nanarum** A. Gentry, from Nicaragua; **M. peytonii** A. Gentry and **M. vasquezii** A. Gentry from Peru; and **M. solomonii** A. Gentry from Bolivia are described.

A number of undescribed species of *Meliosma* have been encountered in the process of preparing the familial treatments of Sabiaceae for the Floras of Nicaragua and Peru and in the course of general identification. *Meliosma* is a largely warm-temperate to montane-tropical genus with at least 15 Asian and ca. 40 neotropical species. A characteristic but rather nondescript element of many Latin American cloud forests, it is very poorly collected and as a result is poorly known taxonomically. Indeed this paper presents the first report of the genus for Peru. Each of the new species proposed here is represented by several collections, making possible an assessment of patterns of intraspecific variability. In addition to these six species, there are many unidentified *Meliosma* collections, especially from Peru, that seem to fit none of the described taxa and may belong to as many as ten or more additional new species. Alternatively these additional collections might represent many fewer relatively polymorphic taxa. I have refrained from describing further presumably new taxa in hopes that future collections will provide clearer understanding of specific delimitations.

Meliosma hartshornii A. Gentry, sp. nov. TYPE: Costa Rica. Heredia: road to Volcán Barba, 2 km N of Sacramento, 2,750 m. alt, 29 Dec. 1974, *G. Hartshorn 1608* (holotype, MO).

Arbor usque 15 m alta. Folia oblanceolata vel anguste elliptica, usque 11 cm longa et 4 cm lata, domatiis axillaribus pubescentibus. Inflorescentia sparsim adpresso-puberula, pedicellis 1–2 mm longis, florum sepalis 1.5 mm longis, petalis ca. 2 mm longis. Fructus globosus, 0.8–1.0 cm diametro.

Tree to 50 cm dbh and 15 m tall; branchlets somewhat angled, glabrous or with a few minute and inconspicuous reddish trichomes, the bark finely longitudinally ridged, with scattered raised lenticels. Leaves alternate to irregularly clustered, oblanceolate to narrowly elliptic, 2–11 cm long, 1–4 cm wide, acute to apiculate at apex, cuneate and often somewhat marginally inrolled at base, coriaceous, the 2° and 3° venation subprominulous above and below, the surface minutely and densely punctate above and lepidote-punctate below, glabrous above and below except for conspicuous tufts of simple trichomes in the axils of the lateral nerves below, drying grayish-olive above, olive or brownish-olive with tan main veins below; petiole 0.2–1 cm long. Inflorescence pyramidal-paniculate with a well-developed central axis, 8–17 cm long, usually opposed to a subterminal leaf or short branch, appearing more or less terminal, glandular-papillose and also sparsely appressed-puberulous, the thick pedicels 1–2 mm long. Sepals 5, ovate, ca. 1.5 mm long, glandular-papillose, the margin strongly ciliate; petals mostly caducous and missing on type, ca. 2 mm long; stamens with slender 2 mm long filament, the bottom half fused with the bottom half of the narrow inner petal, the anthers subglobose, ca. 0.6 mm long, subtended by the thickened connective; ovary ovoid, ca. 1 mm long, densely puberulous, the style linear, 1 mm long. Fruit red when fresh, globose, 0.8–1.0 cm in diameter, not stipitate, sparsely puberulous with flexuous trichomes when young, essentially glabrate, 1-seeded, 0.8–1.0 cm in diameter.

Apparently endemic to the cloud forests of Volcán Barba between 2,700 and 2,800 m.

Additional collection examined. COSTA RICA. HEREDIA: road to Volcán Barba, 1.5 km N of Sacramento, 2,700 m; tree 50 cm dbh, 15 m tall, fruit red, 27 Jul. 1975, *Hartshorn 1759* (MO).

[1] The field work that resulted in discovery of several of the new species described here was supported by grants from the National Science Foundation (DEB-75-20325; DEB-8006253) and USAID (DAN-5542-G-SS-1086-00).

[2] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

This species is distinctive in the genus in its small leaves and smallish fruits. It is closely related to *M. irazuensis* Standl., known only from the type from Volcán Irazú. The main difference is in the larger, pedicellate flowers of *M. hartshornii* as opposed to the tiny (<1 mm long) sessile flowers of *M. irazuensis.* The inflorescence of *M. irazuensis* differs in being narrower, having simple lateral branches with more crowded sessile flowers, and, especially in the very different, much denser pubescence of erect reddish trichomes. Vegetatively that species apparently can be distinguished from *M. hartshornii* by its narrower oblanceolate leaves and pubescent young branches. Another small-fruited, usually small-leaved relative of *M. hartshornii* is *M. idiopoda* Blake, common at somewhat lower elevations in Costa Rica and Chiriquí. The material of *M. hartshornii* was originally identified as a variant of *M. idiopoda,* but its much thicker inflorescence branches and pedicels, larger flowers, thicker more coriaceous leaves, and consistently larger fruits distinguish it from that species.

Meliosma corymbosa A. Gentry, sp. nov. TYPE: Nicaragua. Matagalpa: Cordillera Dariense near Aranjuez, 15 km N of Matagalpa, 1,400 m alt., lower montane moist forest; tree 20 m, 12 Aug. 1977, *Neill 2342* (holotype, MO; isotypes, HNMN, to be distributed).

Arbor usque 20 m alta. Folia oblanceolata vel anguste elliptica, 5–13 cm longa, 1.4–4 cm lata, glabra. Inflorescentia terminalis, corymboso-paniculata, puberula, florum sepalis minus quam 1 mm longis. Fructus asymmetrice subglobosus, 1.6–1.8 cm longus, 1.5–1.6 cm latus.

Tree 20 m tall, the branchlets somewhat angled, glabrous, the bark very finely longitudinally ridged. Leaves irregularly arranged, in part opposite or subopposite, always in part clearly alternate, oblanceolate to very narrowly elliptic, 5–13 cm long, 1.4–4 cm wide, acute at apex, narrowly cuneate at base, coriaceous, entire, drying dark above, olive brown below, the lateral veins plane and inconspicuous above, prominulous below, completely glabrous except for a very few scattered and inconspicuous lepidote or stellate-lepidote trichomes below; petiole slender, indistinctly demarcated from the tapering leaf base, ca. 0.5–2 cm long, glabrous except for a very few minute and inconspicuous scales. Inflorescence terminal, corymbose-paniculate, flat-topped and greatly exceeding the uppermost leaves, dense, puberulous with tiny suberect, reddish trichomes, ca. 10 cm long and 15 cm across, the flowers ultimately on short pedicels, mostly ca. 1–2 mm long. Sepals 5, ovate, minute, less than 1 mm long, glandular-lepidote, the margin minutely ciliate; outer petals broadly ovate, ca. 2 mm long but the rounded apex inrolled, ca. 1.5 mm wide, the inner ones narrow, ca. 2 mm long; fertile stamens 2, the anther thecae thick and suborbicular, ca. 0.5 mm long, subtended by the broad connective; staminodes 3, ca. 1 mm long; ovary ovoid, ca. 1 mm long, merging with the short style. Fruit asymmetrically subglobose, 1.6–1.8 cm long and 1.5–1.6 cm wide, short-stipitate, minutely glandular-papillose, otherwise glabrous, 1-seeded.

Apparently endemic to the montane forests of north central Nicaragua in Matagalpa and Jinotega Provinces.

Additional collections examined. NICARAGUA. MATAGALPA: Macizos de Peñas Blancas, SE side, N of Hda. San Martín, 13°14–15′N, 85°39′W, 950–1,000 m alt., border with Jinotega, 24 Nov. 1981, *W. Stevens & R. Riviere 20916* (MO). JINOTEGA: road from Hwy. 3 to Fundadora, 13°2–4′N, 85°54–55′W, 1,200–1,400 m, large tree in cafetal, 9 Dec. 1983, *Stevens 22542* (MO).

This is a remarkably distinctive species on account of its large corymbose terminal panicle. No other Neotropical species of the genus (and no Asian species represented at MO) has an even remotely similar flat-topped inflorescence; all other species have pyramidal (or variously reduced) inflorescences. In general aspect flowering collections of *M. corymbosa* somewhat resemble some species of *Viburnum* much more than any *Meliosma.* The first collection of this species was filed at MO for some time as a familial "indet." and at first I suspected that it might not belong to Sabiaceae at all. However, the flowers and fruits are undoubtedly the highly distinctive ones of *Meliosma.*

Meliosma nanarum A. Gentry, sp. nov. TYPE: Nicaragua. Zelaya: Cerro El Hormiguero, west range, ca. 13°44′N, 85°00′W, 1,100–1,183 m, dense virgin elfin forest, tree ca. 7 m, fruit pendent, green, 15 Apr. 1979, *J. Pipoly 5169* (holotype, MO; isotypes, HNMN, to be distributed).

Arbor 6–15 m alta. Folia oblanceolata vel anguste elliptica, 3–16 cm longa, 1.2–4.5 cm lata, plus minusve glabra. Inflorescentia ramiflora, pyramidato-paniculata, sparsim adpresso-puberula. Fructus obpyriformis, 1.7–2 cm longus, 1.3–1.9 cm latus.

Tree 6–15 m tall, the branchlets rather thick and crooked, irregularly angled, glabrous or with a few appressed trichomes at extreme tip, with a few scattered large raised round lenticels. Leaves alternate to clustered, oblanceolate to narrowly elliptic, 3–16 cm long, 1.2–4.5 cm wide, acute to short-acuminate at apex, cuneate at base, coriaceous, entire, the venation plane above, intricately prominulous below, essentially glabrous, sometimes with a very few appressed trichomes scattered along midvein below, the surface densely and minutely papillose-glandular, drying dark gray above, brownish below; petiole slender, 1–2 cm long. Inflorescence (in fruit) from below the leaves, rather small, ca. 9–15 cm long, pyramidal-paniculate, with thick well-developed central axis, sparsely minutely appressed-puberulous. Flowers not seen. Fruits obpyriform, 1.7–2 cm long, 1.3–1.9 cm wide, with the poorly demarcated thick basal stipe having a conspicuous asymmetric squarish corner at base, glabrous except for some scales, drying rather light brown.

Apparently locally endemic in the cloud forests of the isolated Cerros La Pimienta and Hormiguero of Zelaya Province, Nicaragua, where it is reported to be locally very common.

Additional collections examined. NICARAGUA. ZELAYA: Cerro La Pimienta, N slope facing La Garrapata, 13°45′N, 84°59′W, 900–1,180 m, cloud forest and lower elfin forest; tree 6 m, frt. green, common in lower elfin forest, 16 Mar. 1980, *J. Pipoly 6049* (MO); Cerro La Pimienta, eastern range, 13°45′N, 84°59′W, 900–1,160 m, tree 7 m, lower elfin forest, fruit green, majority fruiting, locally common, 17 Apr. 1969, *J. Pipoly 5258* (MO); Cerro El Hormiguero, 800–1,000 m, 13°44′30″N, 84°59′30″W, arbol 15 m, frutos verdes, 14 Apr. 1979, *A. Grijalva 318* (MO).

This is a rather nondescript species characterized by small leaves similar in size to those of *M. idiopoda* Blake or *M. matudae* Lundell but more coriaceous. However, the fruits of *M. nanarum* are much larger than those of other small-leaved species and in size approach those of *M. glabrata* Urb. or *M. occidentalis* Cuatr., which differ not only in their larger more membranaceous leaves but apparently also in a thicker fleshier fruit.

Meliosma peytonii A. Gentry, sp. nov. TYPE: Peru. Cuzco: Urubamba, Machu Picchu 0.5 km N of junction of Sayacmarca and Aobamba Rivers, 2,410 m, humid low montane subtropical forest on a ridgeline, 13 Oct. 1982, *Peyton & Peyton 1483* (MO).

Arbor 5–10 m alta. Folia oblanceolata, plerumque 13–29 cm longa, 4–9.5 cm lata, domatiis axillaribus pubescentibus. Inflorescentia paniculata, sparsim puberula. Fructus asymmetrice subglobosus, 1.5–1.8 cm longus, 1.3–1.6 cm latus.

Spindly tree 5–10 m tall, the branchlets somewhat angled, glabrous or glabrescent except for a few minute scales, the surface grayish, very finely striate-ridged, with scattered raised lenticels. Leaves clearly alternate, oblanceolate, (5–)13–29 cm long, (1.6–)4–9.5 cm wide, rounded but often subapiculate at apex, cuneate at base, coriaceous, essentially entire to sharply but shallowly serrate, drying olive brown to grayish above and below, the main veins more or less impressed above and raised below, the surface papillate above, scattered lepidote-glandular below, with conspicuous tufts of trichomes in axils of lateral nerves below, otherwise glabrous; petioles well demarcated, thickened at base, 1–3 cm long. Inflorescence (seen only in fruit) paniculate, axillary and terminal, glabrescently puberulous, the fruits subsessile on short thick woody pedicels. Flowers not seen. Fruits yellow-green turning red when ripe, asymmetrically subglobose, 1.5–1.8 cm long, 1.3–1.6 cm wide, slightly contracted into a very broad and poorly demarcated basal stipe, the surface glabrous, papillate-glandular.

Apparently endemic to the Machu Picchu area of the middle Urubamba Valley, between 2,100 and 2,400 m.

Additional collections examined. PERU. CUZCO: Urubamba, Machu Picchu, 0.5 km N of union of Sayacmarca and Aobamba Rivers, 2,350 m, 11 Oct. 1982, *Peyton & Peyton 1472* (MO); above first waterfall of Río Mandor, 2.5 km from Machu Picchu, 2230 m, *Peyton & Peyton 431* (MO).

This tree is reported by B. Peyton (pers. comm.) to be one of the most commonly occurring trees in his study areas in the narrow belt of low, very humid montane forest between 2,100 and 2,300 m around Machu Picchu and in the nearby Lucumayo drainage. Field notes indicate that the species is often climbed or marked by spectacled bears and B. Peyton (pers. comm.) suspects that these bears eat its fruits.

A second sheet of *Peyton & Peyton 431*, though superficially very similar to the fertile one, apparently consists of part of a compound leaf of a *Cupania* and is not included in the above description.

This species is closest to *M. frondosa* Cuatrec. & Idrobo in vegetative characters but that species has closer together, less strongly ascending sec-

ondary veins, a black-ripening fruit, and less tapered leaf base.

Meliosma solomonii A. Gentry, sp. nov. TYPE: Bolivia. La Paz: Provincia Nor Yungas, valley of Río Coroico, Sacramento, 10 km NE of Chuspipata, 2,450 m, dense ridge-top cloud forest, 67°48′W, 16°18′S. Tree 6 m, flowers white, 27 Jan. 1984, *Gentry & Solomon 44710* (holotype, MO; isotypes, LPB, MO, to be distributed).

Arbor usque 6 m alta. Folia lanceolata vel anguste elliptica, 5–19 cm longa, 1–3.9 cm lata, praeter squamas lepidotas glabra. Inflorescentia pyramidato-paniculata, sparsim puberula, florum sepalis 2 mm longis, petalis 2 mm longis. Fructus ignotus.

Tree to 6 m tall, the branchlets somewhat angled to subterete, puberulous with short stiff ascending hairs when young, glabrescent and glandular-punctate when older, finely longitudinally ridged and with scattered raised lenticels. Leaves alternate, usually irregularly arranged and clustered, lanceolate to very narrowly elliptic, 5–19 cm long, 1–3.9 cm wide, acute to acuminate at apex, cuneate at base, coriaceous, mostly entire, sometimes in part remotely dentate at least toward apex, drying olive to brownish-olive above, brownish below, the secondary veins raised below, plane and inconspicuous above, completely glabrous below except for scattered lepidote glands, above glabrous except for a few scales and reddish trichomes on the deeply impressed midrib; petiole slender at apex, thicker at base, 0.7–1.8 cm long, grooved and puberulous adaxially. Inflorescence terminal and axillary in uppermost leaves, pyramidal-paniculate with an angled well-developed central axis, sparsely puberulous with short subappressed trichomes, with triangular-subulate 1–3 mm long bracts subtending each branch, the individual flowers subtended by a triangular bracteole ca. 1 mm long, subsessile or with a 1 mm long pedicel. Sepals 5, broadly ovate, ca. 2 mm long, glabrous except for ciliate margin; petals broadly ovate, ca. 2 mm long; stamens with slender 1 mm long filaments, fused at base with the small narrow bifid inner petal, the anthers small, widely separated by the thickened connective, including connective ca. 0.5 mm broad; pistil 1 mm long, the ovary ovoid, glabrous, ca. 0.5 mm long, tapering to a linear style ca. 0.5 mm long. Fruit not known.

Known only from the steep slopes of the Coroico valley where it is a common component of the cloud forest, especially on ridge-tops, averaging about 30 plants ≥2.5 cm dbh per hectare.

Additional collections examined. BOLIVIA. LA PAZ: (both from type locality), 29 Jan. 1984, *Gentry & Solomon 44775* (LPB, MO), *44786* (LPB, MO).

Only the second species of Sabiaceae known from Bolivia, *M. solomonii* is very different from *M. boliviensis* Cuatrec., which has much larger reddish pubescent leaves. The new species is characterized especially by the unusually small, lanceolate to very narrowly elliptic, coriaceous leaves, which are similar in size and shape to (but more coriaceous than) those of *M. sellowii* Urban of coastal Brazil. The other small-leaved Andean species of *Meliosma* (*M. tachirensis* Steyerm. & A. Gentry (ined.), *M. meridensis* Lasser) have denser inflorescences, as does mostly lowland *M. herbertii* Rolfe (Antilles and Venezuela). Colombian and Venezuelan *M. meridensis* (which should include *M. uberrima* Idrobo & Cuatrec.) is most similar in leaf texture to *M. solomonii* but its leaves have rounded or obtuse apices.

Meliosma vasquezii A. Gentry, sp. nov., TYPE: Peru. Loreto: Provincia Maynas, Caseria Alianza, Río Tamshiyacu, non-inundated forest on lateritic soil, trail toward Río Manití, 140 m alt., 72°58′W, 4°5′S, 1 Aug. 1980, *Gentry, Vasquez, Jaramillo, Andrade & Stern 29270* (holotype, AMAZ; isotypes, AAU, F, G, IBE, MO, NY, USM).

Arbor 12–20 m alta. Folia obovata, 17–35 cm longa, 7.5–15 cm lata, saltem infra sparsim puberula. Inflorescentia laxa paniculata, saltem 30 cm longa, puberula. Fructus oblongo-obovoideus, 2–2.4 cm longus, 1.5–2 cm latus.

Tree 12–20 m tall, the branchlets somewhat angled to terete, finely puberulous. Leaves clearly alternate, obovate, acuminate, 17–35 cm long, 7.5–15 cm wide, the acumen to 2.5 cm long, the base cuneate, chartaceous, rather remotely sharply serrate, drying dark above, brownish below, the main veins subplane to slightly impressed above, prominently raised below, the tertiary venation plane above, prominulous below, glabrous above except on midvein and sometimes on secondary veins, below puberulous along veins and sparsely over surface; petiole 3.5–6 cm long, rather densely puberulous with suberect reddish trichomes. Inflorescence (seen only in fruit) large, openly paniculate, to at least 30 cm

FIGURE 1. New *Meliosma* species.—A, B. *M. solomonii* A. Gentry.—A. Flowering branch (line is 2 cm).—B. Close-up of portion of inflorescence (line is 5 mm) (*Gentry & Solomon 44710*). C. *M. vasquezii* A. Gentry (line is 2 cm) (*Gentry et al. 29270*).

long, somewhat persistently puberulous, the fruits on thick woody pedicels. Flowers not seen. Fruits turning black, sessile, oblong-obovoid, 2–2.4 cm long, 1.5–2 cm wide, glabrous.

Widespread but rarely collected in lowland Amazonian Peru.

Additional collection examined. PERU. LORETO: Varadero de Mazán from Río Amazonas to Río Napo, 22 Aug. 1972, *Croat 19444* (MO).

This is one of the largest-leaved and largest-fruited species of the genus. In addition to the large leaf size it is characterized by the very long petioles and rather thin leaf texture. It is one of the very few species of the genus that reach lowland Amazonia. Perhaps as many as three other similarly large-leaved but more glabrescent species of *Meliosma* have been collected in lowland Amazonian Peru and Ecuador. One of these, which may be conspecific with Venezuelan *M. aristeguietae* Steyerm. & A. Gentry (ined.), differs in a smaller (1.5 cm diameter) conspicuously keeled fruit as well as in vegetative characters; another, which may be conspecific with Panamanian and Costa Rican *M. allenii* Standley & L. Williams, has entire leaves and a tendency toward parallel tertiary venation.

The Croat collection was originally determined as *Licania egleri* (Chrysobalanaceae), and duplicates were distributed under that name.

NOTES

MORE ON THE TECHNIQUES FOR COLLECTING AQUATIC AND MARSH PLANTS

In 1980 we collected aquatic plants in the vicinity of Vancouver, British Columbia. We were accompanied by Robert R. Haynes and shared with him the joy of collecting aquatics from floristically rich lakes. There were many unforgettable moments. When we read Haynes' recent paper (Haynes, 1984), however, we were surprised to discover the difference between our collecting philosophy and techniques and those he described. We cannot refrain from making a few comments.

1. We do not agree with Haynes' notion, that "if the specimen cannot be determined, it might as well be left in nature." No new taxa would ever be described if one took this notion literally. Although Haynes does not qualify his statement, his instructions are meant "for persons collecting in predominantly tropical areas" (R. R. Haynes, pers. comm.). While we agree that in floristically rich areas it is usually difficult to identify sterile specimens of aquatics, in the temperate zone and floristically poorer areas the situation is simpler. Collectors should not be discouraged, but rather encouraged to collect sterile specimens of those aquatic plants that they cannot find in bloom or fruit.

Many aquatic plants do not flower often. Of the approximately thirty localities of *Megalodonta* (*Bidens*) *beckii* known in British Columbia, there are only two where one finds the species in flower regularly. Although it may be difficult to identify sterile *Megalodonta* using identification keys, someone with an experienced eye can easily make a determination. We have seen only one flowering specimen of *Heteranthera dubia* in British Columbia (where it is known to occur in about fifteen localities) but again, with experience, one can easily identify sterile specimens.

The identification of sterile specimens can be difficult in critical groups, but alternative determination methods can be developed for sterile specimens of aquatics. The anatomical characters of the stem were used to identify broad-leaved species of *Potamogeton* (Ogden, 1943), and minute microscopic characters, such as hairs inside bladders, for identification of *Utricularia* (Komiya, 1972). Different flavonoid patterns of morphologically similar taxa were reported for *Potamogeton* (Haynes & Williams, 1975), *Elodea* (Mues, 1983), *Isoetes* (Kott & Britton, 1982), etc. We used thin layer chromatography of flavonoids for routine identifications of *Myriophyllum* (Ceska, 1977; Ceska & Ceska, 1986) and *Ceratophyllum* (Ceska & Ceska, 1980).

Since one must use destructive methods for identification, or may send duplicate specimens to specialists for their opinions, it is necessary to collect *more* specimens of sterile aquatic plants than of plants in flower. With more material there is a better chance for identification. Of course, before you collect sterile material you should look around the site carefully for plants having flowers or fruits.

In some cases it is important to keep cultures of living aquatic plants. The formation of floating leaves of *Batrachium* can be induced in culture (Cook, 1966), members of Lemnaceae are relatively easy to keep and study in cultures (cf. Landolt, 1980), and temporary cultures are often required in order to get root tips for chromosome counts. On the one hand, one should be equipped with enough collecting supplies ("ziploc" plastic bags, vials, etc.), on the other, one should not collect more taxa than it is possible to accommodate in the available aquaria or culture flasks.

2. A collecting pole is a must. Ours was constructed from an aluminum pike-pole (also known as a boat-hook) which is generally used for handling logs in water sorting grounds or saw mill ponds. It is about 3 m long and 3 cm in diameter. The iron hook at the end of the pole was replaced by a small three-toothed garden weeding fork. The pole is sturdy, but not heavy. In fact, it is made to float on water when dropped, whereas an ordinary garden rake would sink to the bottom. It fits inside a van or on the roof rack of a station wagon. We use the pole every time we collect aquatic plants, whether we do so from shore or a small inflatable boat. C. D. K. Cook (pers. comm.) uses bunches of welding rods welded together in threes at one end. For collecting Lemnaceae, W. P. Armstrong (pers. comm.) uses an aluminum pole with a coffee can attached to the end.

3. Success in collecting depends on whether it is undertaken from shore or a boat. In listing the

flora of individual water bodies, it is important to know the intensity of collecting activities. For this reason we always note whether or not a boat was used, and all adverse factors (rain, wind) that can lower visibility in water.

4. For pressing, most aquatic plants should be floated. Haynes described the technique in sufficient detail. However, always use a pan (a photographic tray, 14 × 18 inches), and do not use newspaper for floating the plants on. Use acid free paper, either mounting paper or white paper of slightly lower weight. Most of the plants do stick to base paper, which can then be glued easily on a regular mounting paper to make a permanent herbarium specimen. Use only clean water for floating and gently rinse the specimens in another tray or bucket before floating them onto the sheet of paper.

5. Avoid the use of chemicals (alcohol, glycerol, etc.) for the treatment of plants before pressing. Plant pigments, which can provide useful information on specimens, are dissolved in organic solvents and lost (cf. Coradin & Giannasi, 1980). Also, do not use drastic pest control measures, such as dipping the specimen into a mercury-chloride solution, in the herbarium. We found that mercury-chloride treatment destroys flavonoids in dried specimens and makes them useless for chromatographic investigations.

6. Specimens of floating Lemnaceae can be prepared easily using the following technique. Wash the collected mass of plants gently and let them spread on water in a tray or small bowl. Take a sheet of dry writing paper of a suitable size (index card format is the best, two or four sheets fit onto a herbarium sheet) and lay it gently on the surface of the duckweed plants. Peel the sheet from the surface of the water and most of the floating plants (about 70 percent) will stick to the surface of the paper in a single layer. Put the sheet with the plants in between newspaper drying sheets and dry in the normal fashion. One can repeat this peeling of duckweed plants several times with new sheets of paper, but the yield diminishes with every repetition.

Dried specimens of Lemnaceae can easily fall off base paper. In the herbaraium they have to be protected in cellophane envelopes or, as W. P. Armstrong (pers. comm.) suggests, in transparent plastic sleeves inserted into manila envelopes mounted on herbarium sheets.

W. P. Armstrong (pers. comm.) also recommends preserving duplicate specimens of *Wolffia* in 70–90 percent ethanol, since the shape and size of fronds are critical characters. He does not recommend using formalin because the fronds become very fragile.

At this point it may be useful to draw attention to an ingenious technique for photographing Lemnaceae and other small floating plants. Witham (1972) published excellent photographs of these plants by floating them in a tray of milk(!), which provided a neutral white background with no shadows or reflections. For their photographs Armstrong (1984) and Armstrong and Thorne (1984) used a dissecting microscope and substage lighting with a fluorescent illuminator to produce a white background and excellent details of diagnostic characters (W. P. Armstrong, pers. comm.).

Collecting aquatic plants can be a rewarding experience when the resulting specimens are more than a blob of dried plant material on a mounting sheet. The preparation of aquatic plant specimens requires more care than that of dry land plants. This effort is repaid, however, because it facilitates the handling and study of the specimens. Each collector tends to develop his own collecting style and in this process practice is more important than a set of guidelines. We will be grateful, however, if our discussion paper helps anyone interested in aquatic plants to develop good collecting habits.

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CHROMOSOME NUMBER IN SARCOLAENACEAE

Sarcolaenaceae are a family of ten genera[1] and approximately 35 species, the living members of which are endemic to Madagascar (Cavaco, 1952; Capuron, 1963, 1970, 1973). The very distinctive tetrad pollen of the family is also recorded from the early Miocene of southern Africa (Coetzee & Muller, 1984). We report here the first chromosome counts for Sarcolaenaceae, the family previously unknown cytologically (Raven, 1975; Goldblatt, 1981, 1984). Based on counts from root tips, obtained from germinating seedlings, we have determined a chromosome number of $2n = 22$ in two species of *Sarcolaena* and one of *Leptolaena*.

The systematic position of the Sarcolaenaceae is not certain but currently the family is believed to be a member of Malvales (Takhtajan, 1980; Dahlgren, 1983). Takhtajan has suggested that it is related to Tiliaceae and Dipterocarpaceae. The Malvales as circumscribed by Takhtajan (1980) share many features with Flacourtiaceae (Violales) as well as with the primitive members of the Theales, especially Ochnaceae. Cronquist (1981) treated Sarcolaenaceae as transitional between Theales and Malvales while Hutchinson (1973) placed Sarcolaenaceae in Ochnales, an order that he considered to be derived from Theales. Recent bark and wood anatomical studies of Sarcolaenaceae (den Outer & Vooren, 1980; den Outer & Schütz, 1981) do not support a close relationship with Ochnaceae, but do suggest that Sarcolaenaceae are placed best in Malvales sensu Takhtajan. Thus despite the difference of opinion concerning the systematic position, Sarcolaenaceae are consistently considered to belong near or to be derived from Theales.

Chromosome number appears to have little to contribute to the understanding of the relationships of Sarcolaenaceae. It is, however, worth restating (after Raven, 1975) the broad cytological patterns in the orders Malvales and Theales. Relatively high base numbers characterize Sterculiaceae, which may have $x = 10$, while reported numbers in Elaeocarpaceae suggest a base number of $x = 14$. Numbers of $n = 18$ and $n = 11$ have been reported from two genera of Scytopetalaceae and Bombacaceae frequently have $n = 36$ and 72, but also $n = 43$, 44, and 48, and possibly $n = 14$ and 28 in *Durio,* the latter two numbers requiring confirmation. Dipterocarpaceae, treated in Theales by Cronquist but more often placed in Malvales (Dahlgren, 1983), have $x = 7$, 6, 11, and 10 (Raven, 1975). Raven concluded that $x = 7$ is possibly basic for Malvales, but that $x = 10$ appears basic for Tiliaceae and Sterculiaceae, possibly an ancient reduction from $n = 14$. Sarcolaenaceae would fit conveniently into this hypothetical reduction series from an early polyploid base of $x = 14$ in Malvales. In Theales, high basic numbers of $x = 18$, 15, 11, and 10 characterize many genera of Theaceae, but Raven has suggested that $x = 7$ may be basic for the family and also for Ochnaceae. Thus Sarcolaenaceae would appear to accord as well cytologically with Theales as with Malvales.

Voucher information for the species counted is as follows:

Sarcolaena oblongifolia Gérard $2n = 22$. Madagascar. Prov. Antananarivo. Antananarivo. Cultivated, Parc de Tsimbazaza (original locality unknown), *Dorr 2746* (MO,TAN).

S. multiflora Thouars. $2n = 22$. Madagascar. Prov. Tulear, Fort Dauphin, Forêt de Mandena, *Dorr et al. 3996* (MO,TAN).

Leptolaena bojeriana (Baillon) Cavaco. $2n = 22$. Madagascar. Prov. Fianarantsoa, Col de Tapia, entre Antsirabe et Ambositra, *Dorr et al. 3844* (MO, TAN).

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[1] Capuron (1970) elevated *Leptolaena* Thouars subgenus *Mediusella* Cavaco to generic rank, but he did not validly make the change in rank since he did not provide a full and direct reference to the place of valid publication of the basionym (ICBN, Art. 33.2). The genus is validly published as follows:

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LEPIDIUM SOLOMONII (CRUCIFERAE), A NEW SPECIES FROM BOLIVIA

Lepidium solomonii Al-Shehbaz, which is named after its collector (James C. Solomon), is a species strikingly different in habit and other characters from any of the 42 native South American lepidiums treated by Thellung (1906), Hitchcock (1945), and Boelcke (1964, 1984). It is a dwarf, matted, caespitose plant with a thick caudex, the branches of which are covered with the persistent petioles from previous years, and each branch is a scape with tiny, simple, entire or 1–4-toothed, rosulate, glabrous leaves. The presence of four stamens and appendiculate petal claws are rare features in *Lepidium* L., which characteristically has two or six stamens and unappendaged claws.

Two other South American species, *Lepidium philippianum* (O. Kuntze) Thell. and *L. quitense* Turcz., have four stamens and sometimes simple leaves, but these are very different from *L. solomonii* in habit and in having elliptic fruits and pubescent or puberulent leafy stems. The new species superficially resembles three North American species, *L. nanum* S. Watson, *L. davisii* Rollins, and *L. barnebyanum* Rev., in habit and in possession of simple leaves and exserted styles (Hitchcock, 1936; Rollins, 1948; Reveal, 1967). It is, however, clearly unrelated to any of these. They differ from *L. solomonii* in having six stamens, ovate to elliptic fruits, unappendaged claws, and leafy stems.

Lepidium solomonii Al-Shehbaz, sp. nov. TYPE: Bolivia. Depto. La Paz: Prov. Los Andes, 6.6 km NW of Batallas on the principal road along Lake Titicaca; 16°15′S, 68°33′W; elev. 3,850 m; rocky hillside with *Stipa, Tetraglochin, Caiophora,* and *Baccharis,* 5 Feb. 1984, *J. C. Solomon 11448* (holotype, MO!; isotypes, GH!, LPB). Figure 1.

Herba perennis caespitosa, pulvinata, multicaulis; caudex ramosus, ramis crassis scaposis; folia rosulata, petiolata, lineari vel anguste oblanceolata, 6–17 mm longa, 0.4–0.8 mm lata; petioli persistentes, basi valde complanati, 3.5–6 mm longi; racemi subcorymbosi, sparsiflori, ebracteati; sepala non saccata, 1.5–1.8 mm longa; petala alba, unguiculata, spathulata vel ovata, 2.2–3 mm longa, unguiculis appendiculatis; stamina 4, filamentis basi dilatatis; siliqua orbiculata, retusa, 3.2–3.8 mm longa; stylus breviter exsertus, 0.4–0.5 mm longus; semina exalata, compressa; cotyledones incumbentes.

Caespitose perennial herbs, forming cushions. Caudex thick, branched, densely covered with papery petiole bases from previous years; ultimate branches rosulate, scapose, 1–2 cm long. Leaves petiolate, glabrous, somewhat fleshy; blade linear to narrowly lanceolate or oblanceolate, 6–17 mm long, 0.4–0.8 mm wide, entire or 1–4-toothed, acute or subacute, attenuate at base; midnerve prominent in the proximal half, obscure in the distal one; petioles persistent, strongly flattened, 3.5–6 mm long, 1.5–1.8 mm wide at base. Inflorescence an ebracteate, few-flowered, subcorymbose raceme, 1–1.5 cm long; rachis glabrous; fruiting pedicels 3–5.5 mm long, ascending, straight, winged. Sepals ascending, glabrous, ovate to broadly oblong, 1.5–1.8 mm long, 1.2–1.4 mm wide, broadly white margined, not saccate, equal at the base. Petals white, clawed, spatulate to broadly ovate, 2.2–3 mm long, 1–1.2 mm wide; claws 1–1.2 mm long, with a small adaxial appendage just below the blade. Nectar glands 4, ca. 0.4 mm long, toothlike, opposite petals. Stamens 4, erect, white; filaments dilated at the base, 1.6–2 mm long, the lateral pair as long as or only slightly shorter than median pair; anthers ovate, ca. 0.6 mm long. Fruits glabrous, orbicular, 3.2–3.8 mm long, keeled, retuse and obscurely winged at the apex; sinus 0.1–0.2 mm deep; styles persistent, exserted, 0.4–0.5 mm long. Seeds ovate, minutely reticulate, wingless, compressed, ca. 1.7 × 1.2 mm, only slightly mucilaginous when wet; cotyledons incumbent.

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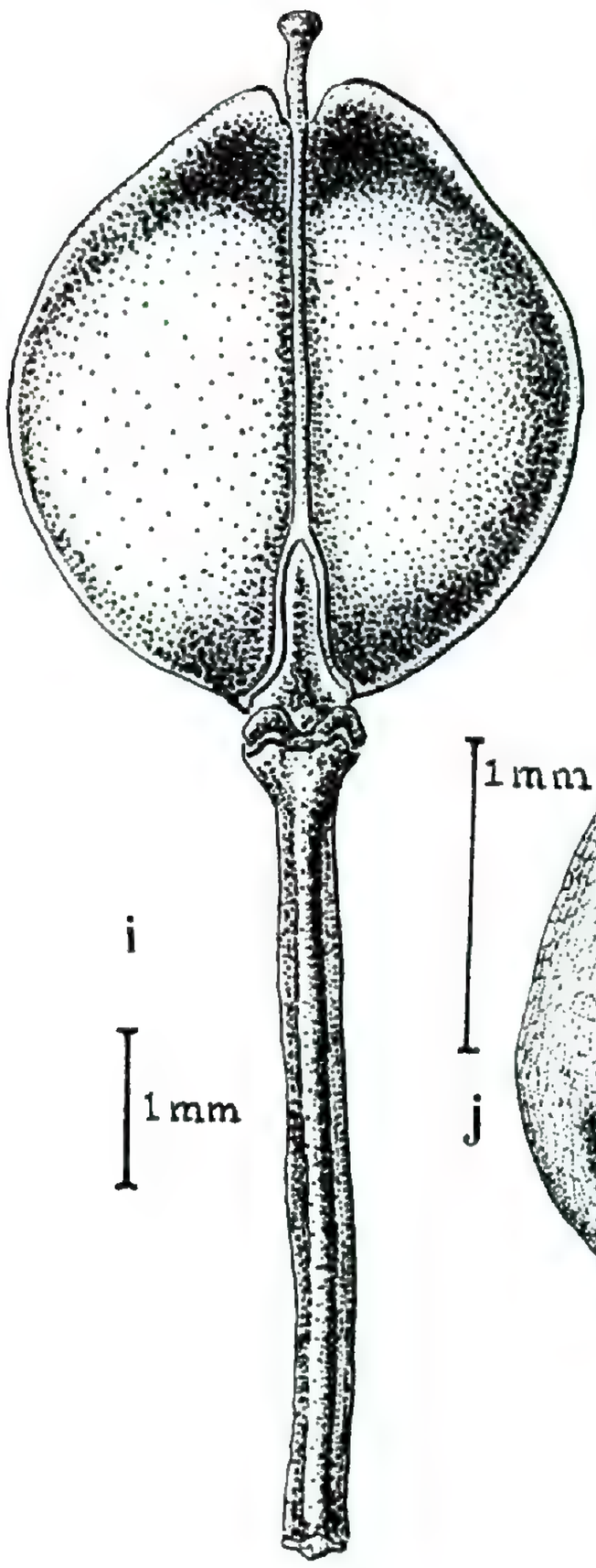

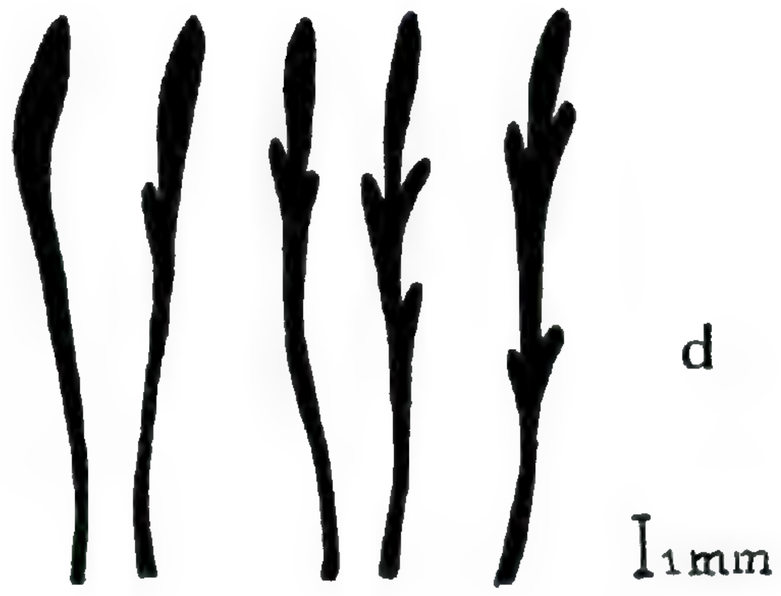

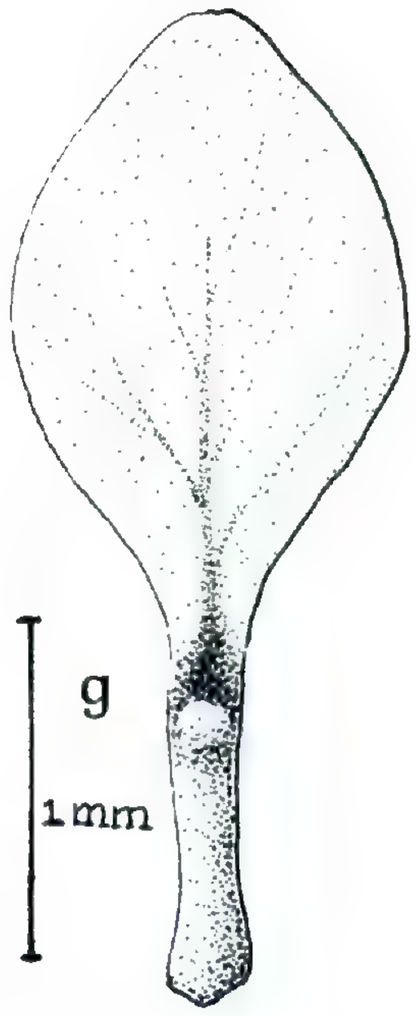

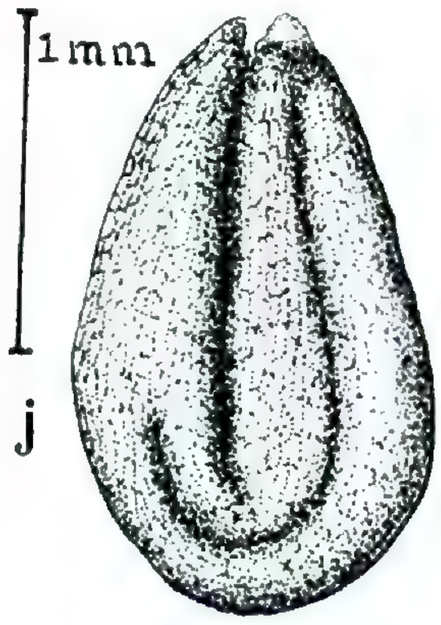

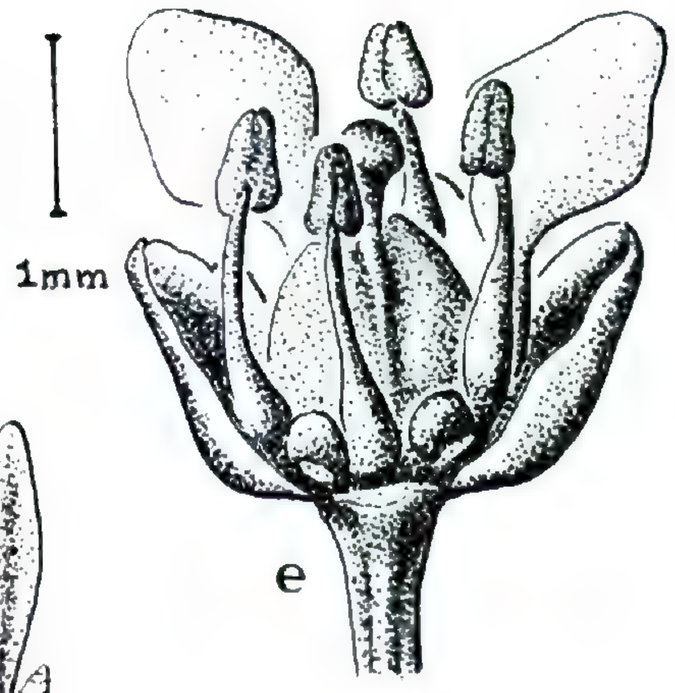

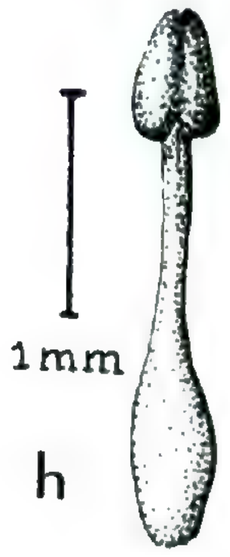

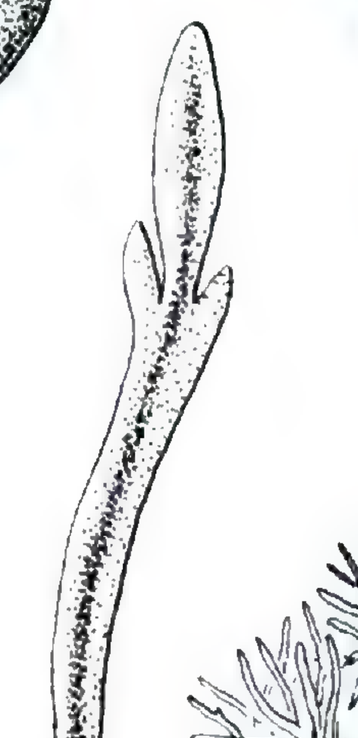

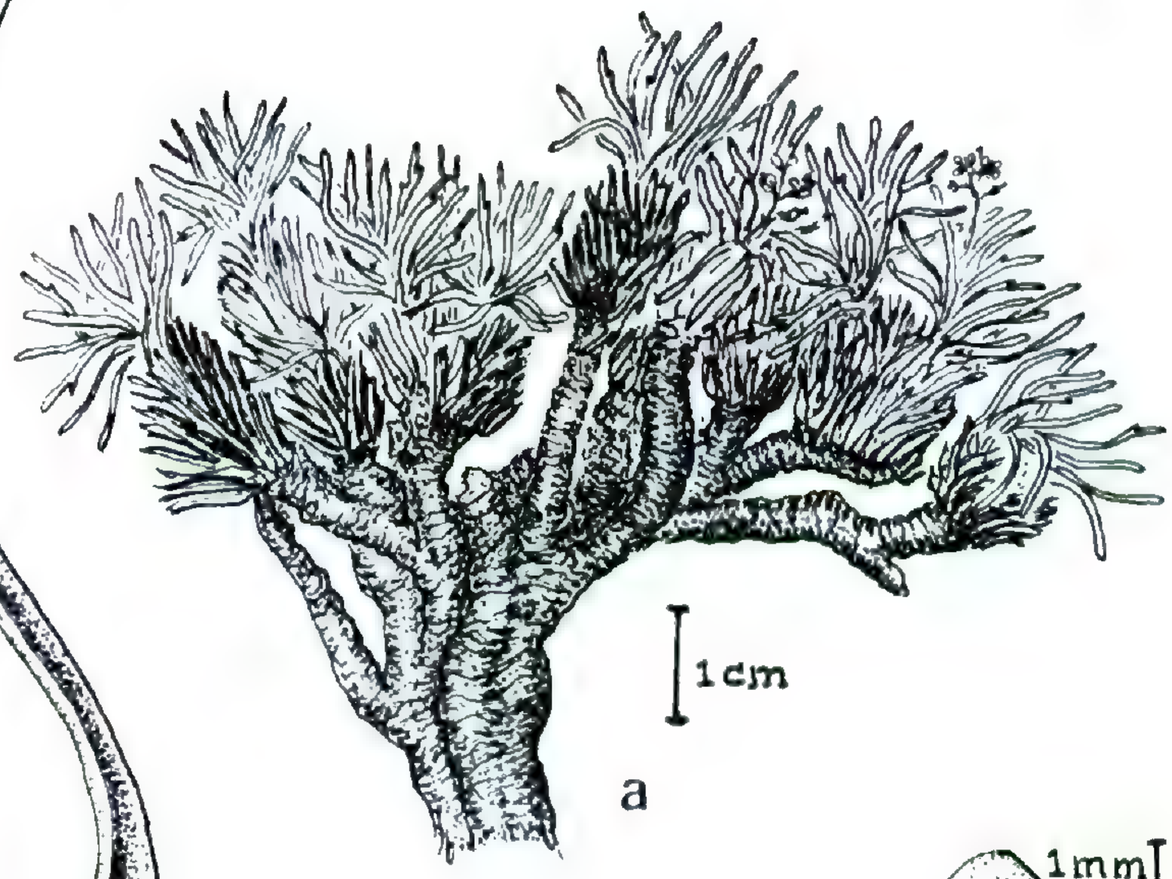

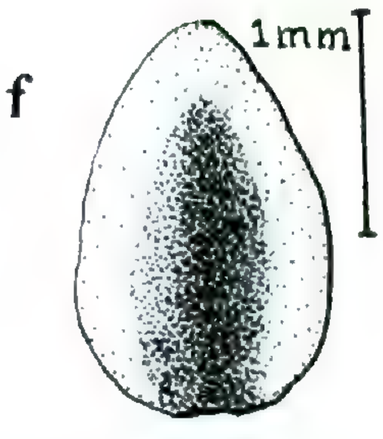

FIGURE 1. *Lepidium solomonii* (from *Solomon 11448*, holotype).—a. Plant.—b. Flowering branch of caudex.—c. Leaf.—d. Variation in leaves.—e. Flower (one sepal and two petals removed).—f. Sepal.—g. Petal.—h. Stamen.—i. Fruit and fruiting pedicel.—j. Seed. (Illustrations by the author.)

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AGOSTINI, GETULIO. (See Sonia Yarsick, Nerida Xena de Enrech, Nelson Ramirez & Getulio Agostini) 99

AL-SHEHBAZ, IHSAN A. *Lepidium solomonii* (Cruciferae), A New Species from Bolivia 830

ARONSON, J. A. (See A. Shmida & J. A. Aronson) 1

AXELROD, DANIEL I. Cenozoic History of Some Western American Pines 565

BAAS, PIETER. (See Shirley A. Graham, Hiroshi Tobe & Pieter Baas) .. 788

BAAS, PIETER. Wood Anatomy of Lythraceae—Additional Genera (*Capuronia, Galpinia, Haitia, Orias,* and *Pleurophora*) 810

BAJAJ, RENU. (See Arthur Gibson, Kevin C. Spencer, Renu Bajaj & Jerry L. McLaughlin) 532

BAKER, HERBERT G. Yuccas and Yucca Moths—A Historical Commentary 556

BOGLE, A. LINN. The Floral Morphology and Vascular Anatomy of the Hamamelidaceae: Subfamily Liquidambaroideae 325

CANNON, J. F. M. (See M. J. Cannon & J. F. M. Cannon) 481

CANNON, M. J. & J. F. M. CANNON. Studies in the Araliaceae of Nicaragua, and a New Widespread Species of *Oreopanax* 481

CARR, GERALD D. & GORDON MCPHERSON. Chromosome Numbers of New Caledonian Plants 486

CESKA, ADOLF & OLDRISKA CESKA. More on the Techniques for Collecting Aquatic and Marsh Plants 825

CESKA, OLDRISKA. (See Adolf Ceska & Oldriska Ceska) 825

CRANE, PETER R. & RUTH A. STOCKEY. Morphology and Development of Pistillate Inflorescences in Extant and Fossil Cercidiphyllaceae .. 382

CRONQUIST, ARTHUR. Commentary on the Status of the Hamamelidae 227

CROSBY, MARSHALL R. Topics in North American Botany, A Symposium Commemorating George Englemann: The Thirty-First Annual Systematics Symposium 503

D'ARCY, W. G. The Calyx in *Lycianthes* and Some Other Genera 117

D'ARCY, WILLIAM G. & ARMAND RAKOTOZAFY. A New Species of *Solanum* (Solanaceae) from Madagascar 498

DILCHER, DAVID L. & MICHAEL S. ZAVADA. Phylogeny of the Hamamelidae: An Introduction 225

DILCHER, DAVID L. (See Michael S. Zavada and David L. Dilcher) 348

DILCHER, DAVID L. & DANIEL MACKLIN. Phylogeny of the Hamamelidae: Taxonomic Index 438

DORR, LAURENCE J. (See Peter Goldblatt & Laurence J. Dorr) 828

DOWD, J. M. (See P. G. Martin & J. M. Dowd) 442

DRANSFIELD, JOHN. A Guide to Collecting Palms 166

ENDRESS, PETER K. Floral Structure, Systematics, and Phylogeny in Trochodendrales 297
ENGELMANN, GEORGE. Instructions for the Collection and Preservation of Botanical Specimens 504
GENTRY, ALWYN H. New Neotropical Species of *Meliosma* (Sabiaceae) 820
GENTRY, ALWYN H. Notes on Peruvian Palms 158
GIANNASI, DAVID E. Phytochemical Aspects of Phylogeny in Hamamelidae 417
GIBSON, ARTHUR, KEVIN C. SPENCER, RENU BAJAJ & JERRY L. MCLAUGHLIN. The Ever-Changing Landscape of Cactus Systematics .. 532
GOLDBLATT, PETER & LAURENCE J. DORR. Chromosome Number in Sarcolaenaceae 828
GOLDBLATT, PETER. Convergent Evolution of the '*Homeria*' Flower Type in Six New Species of *Moraea* (Iridaceae-Irideae) in Southern Africa 102
GOLDBLATT, PETER. Notes on the Systematics of *Hesperantha* (Iridaceae) in Tropical Africa 134
GOLDBLATT, PETER. Cytology and Systematics of the *Moraea fugax* Complex (Iridaceae) 140
GRAHAM, SHIRLEY A., HIROSHI TOBE & PIETER BAAS. *Koehneria*, a New Genus of Lythraceae from Madagascar 788
GRAYUM, MICHAEL H. New Taxa of *Caladium*, *Chlorospatha*, and *Xanthosoma* (Araceae: Colocasioideae) from Southern Central America and Northwestern Colombia 462
HERNÁNDEZ, HECTOR M. *Zapoteca*: A New Genus of Neotropical Mimosoideae 755
HOLSINGER, KENT E. & HARLAN LEWIS. Description of a New Section and Subsection in *Clarkia* (Onagraceae) 491
JONES, JAY H. Evolution of the Fagaceae: The Implications of Foliar Features 228
KAUL, ROBERT B. Evolution and Reproductive Biology of Inflorescences in *Lithocarpus*, *Castanopsis*, *Castanea*, and *Quercus* (Fagaceae) 284
KNAPP, SANDRA. Three New Species of *Solanum* Section *Geminata* (G. Don) Walp. (Solanaceae) from Panama and Western Colombia 738
LANGE, CARLA. (See Michael T. Stieber & Carla Lange) 520
LESTER, RICHARD N. & PHILIP A. ROBERTS. Serotaxonomy of *Solanum*, *Capsicum*, *Dunalia*, and Other Selected Solanaceae 128
LEVIN, GEOFFREY A. Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus 29
LEVIN, GEOFFREY A. Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic Analysis 86
LEWIS, HARLAN. (See Kent E. Holsinger & Harlan Lewis) 491

LOTT, EMILY J. & JAMES S. MILLER. *Bourreria rubra* (Boraginaceae), a New Species from Coastal Jalisco, Mexico 216

MACKLIN, DANIEL. (See David L. Dilcher & Daniel Macklin) 438

MARTIN, P. G. & J. M. DOWD. Phylogenetic Studies Using Protein Sequences within the Order Myrtales 442

MCLAUGHLIN, JERRY L. (See Arthur Gibson, Kevin C. Spencer, Renu Bajaj & Jerry L. McLaughlin) 532

MCPHERSON, GORDON. (See Gerald D. Carr & Gordon McPherson) ... 486

MILLER, JAMES S. (See Emily J. Lott & James S. Miller) 216

MORIN, NANCY R. (See Stanwyn G. Shetler & Nancy R. Morin) 653

PENG, CHING-I. A New Combination in *Ludwigia* Sect. *Microcarpium* (Onagraceae) 490

POHL, RICHARD W. A New *Paspalum* (Poaceae) from Mesoamerica ... 501

RAKOTOZAFY, ARMAND. (See William G. D'Arcy & Armand Rakotozafy) 498

RAMIREZ, NELSON. (See Sonia Yarsick, Nerida Xena de Enrech, Nelson Ramirez & Getulio Agostini) 99

RAVEN, PETER H. (See Hiroshi Tobe & Peter H. Raven) 768

REDFEARN, PAUL L. & P.-C. WU. Catalog of the Mosses of China 177

ROBERTS, PHILIP A. (See Richard N. Lester & Philip A. Roberts) 128

ROMEO, JOHN T. Distribution of Nonprotein Inimo and Sulphur Amino Acids in *Zapoteca* 764

ROMERO, EDGARDO J. Fossil Evidence Regarding the Evolution of *Nothofagus* Blume 276

ROMERO, EDGARDO J. Paleogene Phytogeography and Climatology of South America 449

SHAW, ELIZABETH A. Changing Botany in North America: 1835–1860. The Role of George Engelmann 508

SHETLER, STANWYN G. & NANCY R. MORIN. Seed Morphology in North American Campanulaceae 653

SHMIDA, A. & J. A. ARONSON. Sudanian Elements in the Flora of Israel 1

SMITH, ALAN R. (See Julian A. Steyermark & Alan R. Smith) 209

SMITH, LYMAN B. Revision of the Guayana Highland Bromeliaceae ... 689

SOUSA S., MARIO. Adiciones a las Leguminosas de la Flora de Nicaragua 722

SPENCER, KEVIN C. (See Arthur Gibson, Kevin C. Spencer, Renu Bajaj & Jerry L. McLaughlin) 532

STEYERMARK, JULIAN A. & ALAN R. SMITH. A Remarkable New *Selaginella* from Venezuela 209

STEYERMARK, JULIAN A. *Holstianthus,* a New Genus of Rubiaceae from the Guayana Highland 495

STIEBER, MICHAEL T. & CARLA LANGE. Augustus Fendler (1813–1883), Professional Plant Collector: Selected Correspondence with George Engelmann 520

STOCKEY, RUTH A. (See Peter R. Crane & Ruth A. Stockey) 382

SYMON, D. E. A Survey of *Solanum* Prickles and Marsupial Herbivory in Australia 745

THOMAS, DUNCAN W. Notes on *Deinbollia* Species from Cameroon ... 219

THORNE, ROBERT F. A Historical Sketch of the Vegetation of the Mojave and Colorado Deserts of the American Southwest 642

TIFFNEY, BRUCE H. Fruit and Seed Dispersal and the Evolution of the Hamamelidae 394

TOBE, HIROSHI. (See Shirley A. Graham, Hiroshi Tobe & Pieter Baas) .. 788

TOBE, HIROSHI & PETER H. RAVEN. A Comparative Study of the Embryology of *Ludwigia* (Onagraceae): Characteristics, Variation, and Relationships 768

WAGNER, WARREN L. New Taxa in *Oenothera* (Onagraceae) 475

WU, P.-C. (See Paul L. Redfearn & P.-C. Wu) 177

XENA DE ENRECH, NERIDA. (See Sonia Yarsick, Nerida Xena de Enrech, Nelson Ramirez & Getulio Agostini) 99

YARSICK, SONIA, NERIDA ZENA DE ENRECH, NELSON RAMIREZ & GETULIO AGOSTINI. Notes on the Floral Biology of *Couroupita guianensis* Aubl. (Lecythidaceae) 99

ZAVADA, MICHAEL S. (See David L. Dilcher & Michael S. Zavada) 225

ZAVADA, MICHAEL S. & DAVID L. DILCHER. Comparative Pollen Morphology and Its Relationship to Phylogeny of Pollen in the Hamamelidae 348

Volume 73, No. 3, pp. 503–651 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, was published on 9 February 1987.

Contents continued from front cover

New Neotropical Species of *Meliosma* (Sabiaceae) *Alwyn H. Gentry* 820

NOTES

More on the Techniques for Collecting Aquatic and Marsh Plants *Adolf Ceska and Oldriska Ceska* 825

Chromosome Number in Sarcolaenaceae *Peter Goldblatt and Laurence J. Dorr* 828

Lepidium solomonii (Cruciferae), A New Species from Bolivia *Ihsan A. Al-Shehbaz* 830